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A GROWTH MODEL FOR SALMONIDS REARED IN HATCHERY ENVIRONMENTS

by

GARY DEAN STAUFFER

A dissertation submitted in partial fulfillment
of the requirements for the degree of
DOCTOR OF PHILOSOPHY

UNIVERSITY OF WASHINGTON

1973

Approved by Douglas G. Chapman
(Chairman of Supervisory Committee)

Department Fisheries
(Departmental Faculty Sponsoring Candidate)

Date May 16, 1973

UNIVERSITY OF WASHINGTON

Date: March 2, 1973

We have carefully read the dissertation entitled "A growth model for salmonids reared in hatchery environments" submitted by Gary Dean Stauffer in partial fulfillment of the requirements of the degree of Doctor of Philosophy and recommend its acceptance. In support of this recommendation we present the following joint statement of evaluation to be filed with the dissertation.

Faculty and staff of the Center for Quantitative Science are developing a total systems model of a hatchery salmon run. Such a total model is built up of several components of which the growth of the young salmon during their hatchery phase is a very important element. It is to such a hatchery growth model that this thesis is directed. While this model will be a vital component of the larger model, it has a great deal of value in its own right by its development of better understanding of growth in general and of young salmonids in particular which it is hoped will lead to better hatchery management.

To build his growth model, Stauffer has reviewed the literature on salmon growth thoroughly and he first considers the relevant factors influencing growth. Some of them are not appropriate for modeling and are not considered here. The variables under control of management which are temperature and ration, as well as fish weight, are the primary variables of the model. Stauffer uses basic principles of growth to determine an empirical growth equation involving biologically meaningful parameters. These parameters are then expressed as functions of temperature and weight.

Development of these several equations is a skillful combination of theoretical and empirical models using a variety of data obtained from the literature. To test this model, a computer program GROWTH is developed and is used to simulate growth of coho salmon (Oncorhynchus kisutch) and chinook salmon (Oncorhynchus tshawytscha) using basic data from several hatcheries in Oregon and Washington. These simulated data are compared to the actual growth data without further curve fitting or parameter estimation. The agreement between the model and the actual data is remarkable. It is therefore possible to suggest a number of practical applications for the GROWTH simulator.

Finally, a preliminary sensitivity analysis is undertaken. There are suggestions of further work here as well as in replacing the empirical equations in some places by a functional model. That more work can still be done is not to belittle the accomplishments of the dissertation. This is a major step forward in its field and we recommend acceptance of this dissertation.

DISSERTATION READING COMMITTEE: Douglas G. Chapman

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Doctoral Dissertation

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ACKNOWLEDGEMENTS

I am grateful to my graduate supervisory committee Dean D. G. Chapman (chairman), Drs. G. W. Brown, E. O. Salo, R. R. Whitney, and K. J. Turnbull (graduate school representative) for their assistance, critizism, and encouragement. In particular I thank Dean Chapman for accepting the position of chairman after the death of Prof. G. J. Paulik and Dr. R. R. Whitney for filling the vacant position. I am deeply indebted to Prof. G. J. Paulik for his guidance and teaching throughout my graduate study.

I could not have accomplished my original proposal without the timely work of Dr. J. R. Brett, Pacific Biological Station, Nanaimo, B. C. I am indebted to his insights and presentations. Mr. Joseph Banks, Bureau of Sport Fisheries and Wildlife and Mr. David Leith, Fish Commission of Oregon provided encouragement but most importantly much of the experimental data essential in developing the functions of temperature and weight. I am grateful for their willingness to share their unpublished data. I hope this dissertation is as much help to them in their future work.

I appreciate the suggestions and encouragement of Drs. Peter Bergman, Washington State Department of Fisheries; Kashinath Patil, University of Washington; Robert Parker, Pacific Biological Station, Mr. Fred Johnson, and Tony Rasch.

The benefical discussions with James DeShazo, Charles Fowler, Lars Mobr , and Time Smith should be recognized. The staff of the Fisheries Analysis Center particularly Ms. Helen Bailey deserve many thanks and a bright gold star for their efforts.

The financial support for this research was obtained under the general sponsorship of Quantitative Ecology and National Resource Management Program supported by Ford Foundation Grant no. 68-183.

My wife, Diane, deserves recognition and thanks not only for the usual sacrifices and moral support but also for her many hours of transcribing data and typing the drafts and final copy of this dissertation.

INTRODUCTION

The primary purpose of this dissertation is to develop a mathematical growth model that predicts daily or weekly growth of salmonids in a hatchery environment. Once this is accomplished the model can be used to forecast the growth of salmonids reared in Pacific Northwest hatcheries. The model could also be used to forecast water temperature and food ration schedules that would be required to obtain fish of specified sizes in specified times. The spinoffs from the development of such a growth model are numerous. The model can be used to conduct "dry lab" experiments on a laboratory or production basis to test various hypotheses on the growth response to environmental conditions. By fitting the growth model to the control group of an experiment, one could compare the growth response of a treated group. The treatment may be a particular feeding practice, a diet modification, a chemical treatment for disease or the disease itself, a genetic strain, fish density, type of rearing pond, water quality or even a particular hatchery. If the environment is properly accounted for, then the model could also compare test results between experiments where the growth responses are confounded with the environmental conditions of the experiments. Academically, the development of the model requires piecing together the knowledge of growth in an attempt to understand the plasticity of growth in poikilotherms.

Growth models presented by earlier workers are generally reliable only in situations with constant environment and for time intervals as long as a year. Haskell (1959) proposed a growth equation for hatchery trout that described daily growth, but his model is only adequate for constant environments. Winberg's (1956) energy budget model is fundamental to growth but not enough is known about the influence of the environment on ingestion and metabolism to make it possible to use his model (Warren and Davis, 1967). Paloheimo and Dickie (1965) developed a growth model by extending the energy budget equation. Their model appears to be adequate only for uniform feeding levels over time (Warren, 1971). Also their model implicitly confounds body weight and daily food consumption, which are highly correlated. A growth model that overcomes these problems would have immediate application in the systems model HATCH being developed by Washington State Department of Fisheries to evaluate hatchery rearing and release strategies (Bergman, Mathews, and Paulik, 1972; Rasch, 1972).

Production of trout and salmon in artifical facilities is important in the Pacific Northwest and has all indications of rapidly expanding in the future. The Bureau of Sport Fisheries and Wildlife (Anon., 1968) tabulated a total production of over 257 million fish in Washington and Oregon in 1965. They predicted a production of over 400 million by 1973 and just under 600 million by 1980. The State of California produced 70 million trout and salmon (4 million pounds) at a cost of over 3.5 million dollars for the 1970-1971 fiscal year (Bruley, 1972). In 1969, 2.2 million pounds of trout were produced in 250 trout farms in Norway, 1.6 million pounds more than in 1962 (Anon., 1972).

Improved diets and better disease control are mainly responsible for the increased production of salmonids in artifical facilities (Bardach and Ryther, 1968; Cleaver, 1969). Regulating the temperature of hatchery water can also greatly enhance trout and salmon production. Burrows and Combs (1968) have shown that heating water is feasible for water re-use systems. These technological advances make it possible to rear great numbers of salmon to larger sizes for release at various times of the year.

Available information indicates that survival in the ocean for hatchery reared salmonids is influenced by the average size and release time of the smolts (Wallis, 1968; Cleaver, 1969). Bardach and Ryther (1968) report a specific incident where the return was 7 to 8% for coho salmon (Oncorhynchus kisutch) released as 27 gram smolts compared to 1 to 2% for 13 gram smolts. Johnson (1970) made a similar report on two experimental groups of coho salmon released from Big Creek Hatchery on the Columbia River. The two groups released on the same day averaged 16.6 and 42.5 grams per fish. The overall return to the fisheries and hatchery for the two size groups was 1.8 and 5.7% respectively. If ocean survival is confirmed to be greater for larger sized smolts, policy makers may decide that fish culturists are to rear fish to a larger smolt size to take advantage of this increased survival. For those hatcheries that produce smolts equal to the maximum size attainable under their set of environmental conditions, this policy may be difficult to meet without environmental modifications. Since fish normally respond to environmental changes with changes in their growth pattern, fish culturists can regulate biomass and growth patterns by controlling the hatchery environment. This requires decisions on the levels to adjust the environmental factors such as ration and temperature to achieve the predetermined goals (Brett and Sutherland, 1970).

These decisions and the corresponding ramifications become more complex as environmental control technology becomes more advanced. A system analysis like that involving the systems model HATCH is a feasible approach for sorting through all the possible alternative rearing strategies to find the set of hatchery and environmental conditions such as fish size, ration and temperature schedules, species mix, water requirements, and release times that best achieves the desired results. To use a simulation model like HATCH to evaluate various growth strategies, it must include a growth model that can predict growth reasonably well for the range of the most important environmental factors. This growth model could also be used to predict growth patterns at those facilities that are capable of producing larger smolts with only minor alterations in hatchery procedures such as increasing food rations or delaying release time.

DEFINITION OF GROWTH TERMS

Growth is an orderly but complex physiological process that accumulates energy in an organism through a series of biochemical reactions as briefly outlined by Lehninger (1965). Physiologists prefer to define growth as the synthesis of proteins. Although actual growth occurs at the molecular level which results in increased cellular material, it is easiest to monitor growth of an organism by measuring body weight. For the purpose of this dissertation growth will be thought of as the accumulation of mass and will be measured in grams of body weight. A better measure of growth is the total energy content of the body (Warren and Davis, 1967). Unfortunately growth is only measured this way in the more detailed laboratory experiments. If the proportion of moisture, protein, fat, and carbohydrate in the experimental organisms are constant over time, the two methods give similar results.

For the purpose of this dissertation, the rate of growth is defined as the change in body weight over time, *i.e.*, the first derivative of growth with respect to time, denoted by dW/dt where W = fish weight and t = time. Specific growth rate, g, synonymous with exponential growth rate is defined as the change in body weight per unit of body weight per unit of time, *i.e.*, the rate of growth divided by body weight, denoted by dW/Wdt. In both cases the unit of time particular to this dissertation will be 1.0 day.

Ration, R, refers to the amount of food consumed during some period of time. More specifically ration is defined here as the weight of food consumed by an individual fish per body weight per day (Ricker, 1946). In both cases food consumed and body weight are measured in grams, so that ration is measured as fraction of body weight per day.

A number of terms are used to measure the ability of fish to convert food stuffs into fish flesh. Laboratory scientists usually think in terms of conversion efficiencies while hatchery oriented researchers think in terms of conversion factors. The latter term is the inverse of the former. Following Warren and Davis (1967) and Brett, Shelbourn, and Shoop (1969) gross efficiency of food conversion is defined as the ratio of growth, ΔW, to food consumed, F, during some period of time. This is equivalent to the ratio of specific growth rate to ration as defined above, i.e., gross efficiency = $\Delta W/F = g/R$. Food conversion factor is the inverse, i.e., the ratio of daily ration to specific growth rate. Net efficiency of food conversion is defined to be the ratio of growth to the quantity, ration minus the maintenance ration.

If the maintenance ration, denoted by RMAINT, is defined as that level of ration that maintains a constant body weight, then

$$\text{net efficiency} = g/(R - \text{RMAINT})$$

Net efficiency has no useful meaning when a net decrease in body weight occurs.

A new term that will be referred to later is the marginal efficiency of food conversion. For the moment think of a monotonic function that relates the possible weight of a fish at time t + 1, with the all possible levels of food consumption during the interval t and t + 1. Then for a given level during this time period, say F_1, the fish will grow to some size at t + 1, say W_1. But on the other hand if the food consumption was not F_1 but some other value, say F_2, the fish would grow to a slightly different size, say W_2. Then the marginal efficiency of food conversion is defined as the ratio

$$\left(W_1-W_2\right)/\left(F_1-F_2\right)$$

The weight at time t + 1 can be thought of as some undefined function of F denoted by w_{t+1} (F). The marginal efficiency of food conversion can then be defined as the derivative of w_{t+1} (F) with respect to F. This derivative is approximately equal to the above ratio if the change in F is small, i.e.,

$$dw_{t+1}/dF \approx \left(W_1-W_2\right)/\left(F_1-F_2\right)$$

The concept of marginal efficiency is employed later in an algorithm which estimates the daily ration necessary to achieve some pre-determined fish size.

The intent here is to keep units of measurement compatible with the standard procedures in salmonid hatcheries and related experiments and with those used in HATCH.

FACTORS INFLUENCING GROWTH

Haskell (1959) reviewed the factors that have the greatest influence on growth of trout in hatcheries. His list includes water temperature, care, species, race, diet, feeding level, health, and sexual maturity. Others are social hierarchy, age, size, activity, and photoperiod (season).

Care

Haskell (1959) mentions that care is extremely important for good growth. By care he means "good housekeeping" or proper fish culture practices including feeding techniques, providing adequate water supply, and cleaning ponds regularly. Proper feeding techniques insure minimal wastage of food and maximum ingestion. Adequate water supply provides necessary oxygen and flushes metabolic wastes. Regularly cleaned ponds have minimal algae growth and a low accumulation of metabolic wastes. Since "good housekeeping" is the standard policy for fish culturists (Leitritz, 1959) and since modern facilities are designed to provide the best of care (Burrows and Chenoweth, 1970; Burrows and Combs, 1968), the quality of care will not be considered as input to the growth model. It is assumed that care will be adequate so as not to allow oxygen or metabolic products to reach levels that inhibit growth. More important it is assumed that food wastage is negligible.

Diets

The modern trout and salmon diets are a varied mixture of a variety of meals, oils, mineral and vitamins. The ingredients are selected on the basis of availability, cost, fish requirements, growth performance and survival (European Inland Fisheries Advisory Commission (EIFAC), 1971; Horak, 1971; Hutchens and Nord, 1956; Hublou, 1963; Phillips and Brockway, 1959). The contribution of each organic substance is nearly impossible to evaluate due to the complexity of biochemical interactions that can occur and the ability of the fish to improvise when the quantity of a particular substance is low or zero. Brett (1971b) found considerable differences in growth response of sockeye fingerlings (Oncorhynchus nerka) to a variety of standard diets. For these reasons the growth model is based on those diets most often used in production hatcheries.

Disease

Growth of fish is retarded during disease outbreaks (Haskell, 1959). Needless to say, diseases are not a standard mechanism employed by fish culturist for regulating growth. For this reason, a measure of disease intensity will not be included as input to the growth model. However the fish culturist should consider the potential risk of disease when the environment is altered to achieve some desired growth pattern.

Maturity

Sexual maturity is irrelevant in the cases where fish are released into natural waters early in their life history and will not be dealt with in the development of this growth model. Any extension of the model to the adult life stanza must account for fluctuations in growth resulting from sexual maturity.

Photoperiod

Brown (1946b) briefly examined the influence of photoperiod on the growth of adult brown trout (*Salmo trutta*). The temperatures were held constant at 11.5°C (52.7°F) and the fish were fed *ab libitum* rations of a meat diet once a day. There was no obvious difference in growth between fish reared in 18 hours of light per day and those in 12 hours of light. Fish of a different age reared at 6 hours of light grew considerably larger than similar aged fish reared in 12 hours of light. Unfortunately Brown did not compare food consumption or degree of sexual maturity. Stickney and Andrews (1971) examined the influence of photoperiod on gross efficiency for channel catfish (*Ictalurus punctatus*) where rations were held constant. Apparently efficiency is not altered significantly. Photoperiod though may influence the time of smolting and spawning which in turn may influence growth.

By altering the photoperiod, one might change the normal feeding frequency to a new pattern that achieves a higher daily ration or greater conversion efficiency than was previously possible. Haskell (1959) claims that there is no growth advantage for trout from increased photoperiod once the fish are larger than 0.45 grams (1000 fish/lb). Since the relation between food consumption and conversion efficiency with altered photoperiod is unclear, photoperiod will not be considered an important environmental parameter in controlling growth even though photoperiod can be easily manipulated on an experimental and production basis.

Ration and feeding frequency

The relationship between growth and feeding level or daily ration has been the subject of numerous studies for many years. This work has been successful in delineating the effects of ration on fish growth. This work provides the foundation on which the present growth model is built. Essentially food is the source of energy for fish and the sole driving force for growth.

Associated with the effects of ration on growth is the frequency of feedings during the day. There are many possible strategies for feeding a quantity of food to a group of fish during a day. The extremes are feeding the entire quantity in one short period as opposed to feeding small amounts continuously during daylight hours. A "best" feeding strategy probably exists which results in a minimum of food wastage and the highest conversion efficiency. Estimation of feeding frequency strategies by modelling procedures would require measuring time in units of one hour or shorter. Simulating growth on an hourly basis would consume a larger amount of central processing time on the computer resulting in considerable expense. For the purpose of this dissertation it is assumed that feeding practices are near the optimal strategy, and that daily ration is adequately estimated by the average of weekly food consumption independent of feeding frequency.

Social hierarchy

Brown (1946a) observed differences in growth patterns between individual brown trout under identical conditions in the same aquarium. She was able to attribute these differences to social hierarchy. Fish that grew slowly showed a rapid increase in growth once larger fish were removed. Many species of trout and salmon are known to have territorial behavior (Chapman and Bjornn, 1969). In hatcheries this has been shown to be greatly reduced by the more crowded conditions and abundance of food. Leitritz (1959) warns fish culturists to take extra care in feeding to insure that the smaller and weaker fish receive their portion of the daily ration. Haskell (1959) argues that if a social hierarchy exists in heavily stocked hatchery ponds then it must be of a very transitory character. He claims that over any extended period its effect on the growth of individuals would be negligible. Because of the large numbers of fish raised in a hatchery at any one time and the difficulty of keeping track of individuals in experiments, most of the input data for the growth model represents the average response of a large group of fish.

Species and race

Species and race are factors for which it is difficult to attach some meaningful value that would be characteristic of their effects on growth response without experimenting with each race or species. Species and races can be partially differentiated by egg size or weight of fry at time the yolk sac is completely absorbed (*i.e.*, "buttoned up"). Because of difficulty relating one species or race to another these will not be considered as factors in the growth equation. Although a separate set of coefficients will be considered, if necessary, for the species or races of fish being examined.

Swimming activity and exercise

Swimming activity is physical work and requires energy. If fish do not swim the conserved energy could result in additional growth. The velocity of moving water in large hatchery ponds has not been measured in the past. The major concern was to provide enough fresh water to sustain the population. Leitritz (1959) noted for deep still ponds that fish rested most of the time and food conversions were usually better than in ponds with higher water velocities. He attributed the difference to the greater expenditure of energy for maintaining position in the swifter pond.

Recently investigators have been concerned about the quality of the smolts released. One measure of quality has been physical stamina. A more physically fit individual should be better able to escape predators and therefore have a higher probability of survival (Burrows, 1969; Poston, McCartney, and Pyler, 1969). To increase stamina fish are exercised in relatively fast flowing water. Also with the concept of self-cleaning ponds Burrows and Chenoweth (1970) have been concerned with water currents and velocities which provide the cleaning action as well as exercise. Other than this there is little evidence that water velocities have been employed to control the activity of fish or fishes' use of energy. A major concern has been to keep velocities below maximum that fish can sustain to prevent them from being impinged upon the outlet.

The effect of long term exercising on growth of trout is inconsistent. Phillips and Brockway (1959) exercised brook trout (Salvelinus fontinalis) and brown trout in hatchery raceways by increasing water flow 4 hours daily for 3 months. In one test, exercised brook trout outgrew the controls, in the other test the controls outgrew the conditioned trout. Pyle, Posten, and Livingston (1967) detected no significant difference in the growth between exercised brook trout and the unexercised controls. After 20 weeks an exercised group increased in size from 2.8 grams to 38.9 grams on the average while the controls increased from 2.8 grams to 35.9 grams. The water velocity for the control group was negligible. The test group was exercised at 0.55 feet/sec for 16 hours daily and at an increased velocity for the remaining 8 hours that increased to 1.2 feet/sec by the end of the 20 weeks. Posten, McCartney and Pyle (1969) reported similar results for brook trout in that the exercised fish averaged 22.83 grams as opposed to 20.65 grams for the controls. They attributed this difference to better food distribution resulting from the water flow. In this experiment the water velocities were 0.81 feet/sec for 16 hours daily and 1.15 feet/sec for the other 8 hours.

Brett (1964) found that the maximum velocity sockeye fingerlings could sustain for a period of time was 4 lengths per second. Burrows and Chenoweth (1970) show the relation between fish size and maximum water velocities at which chinook fingerlings (<u>Oncorhynchus tshawytscha</u>) can maintain themselves. Their figure 3 shows that swimming ability increases with size. In order to convert these data from feet per second to fish lengths per second, Haskell's (1999) length-weight table was used to change their number of fish per pound to length of fish in feet. This conversion resulted in an estimate of maximum speed of 4.6 lengths per second for a wide weight range of chinook fingerlings. This number agrees with Brett's (1964) value for sockeye. In studies of rearing pond hydraulics Burrows and Chenoweth (1955 and 1970) found that in a variety of hatchery ponds water velocities varied from zero in dead areas to above those fish can sustain near water inlets.

Brett (personal communication) believes that once water velocities in the typical rearing troughs or ponds are increased above some minimal value that fish can take advantage of the variety of velocities due to turbulence to "glide" along. For a variety of velocities below the maximum sustained speed, he thinks juvenile salmon are capable of maintaining a uniform low level of energy expenditures with no detectable differences in growth. This may not be the case in stamina tunnels where currents are uniform over the entire cross section of the holding chamber.

The available evidence suggests that swimming activity below maximum sustainable speeds affects growth of salmonids only slightly if at all in hatchery environments. With the highly variable water velocities and activity of fish in most hatchery ponds, it becomes quite difficult to assign a reasonable value to swimming activity. For the purpose of this dissertation it is assumed that energy expended for swimming activity is a low uniform value that has a negligible effect on growth.

Size and age

In general specific growth rates of fish vary with size and age. Medawar (1945) presented five growth laws that apply generally to fish, particularly within life stanzas (Brown, 1957). The fifth law says that specific rate of growth decreases at a decreasing rate as a fish increases in age. Also Medawar's first law says that the size of a fish is a monotonic increasing function of its age. It follows then that specific growth rate decreases as fish increase in size and age making age and size confounded factors (Brown, 1946a).

Haskell (1959) reported that growth rates, when measured in units of body length, were independent of fish size for fingerling rainbow trout. The increase in length was a function of the rearing time. Later it will be demonstrated that if the above is true, then the growth rate and the specific growth rate in terms of weight are functions of weight assuming isometric growth. Brett, et.al. (1969) found specific growth rates for sockeye fingerlings were stable during extended periods of time. They concluded that age may be an important factor in determining specific growth rate. Brown (1946a) concluded from her studies on brown trout fry that age is a significant factor in controlling specific rate of growth and that there is no correlation between body weight and specific growth rate.

Experimenters have stopped the growth of fish by reducing daily rations to a maintenance level or lower. After long periods of no growth the fish can resume a normal or above normal growth rate once the rations are increased. During winter months the growth of trout and similar species typically ceases for many months due to the cold water temperatures even though food is plentiful. Growth resumes to normal with the warming of spring (Brown, 1957). It is probably best to treat specific growth rates as a function of fish size rather than age if growth is regulated by changes in the environment.

Temperature

The relationship between growth and water temperature has also been the subject of numerous studies. Workers have been successful in describing major temperature effects on behavior and rates of various biological processes. Temperature plays an important role in regulating rates of digestion and consequently maximum daily food consumption. The rate of metabolism is also partially regulated by temperature and metabolism controls the level of the maintenance ration. The importance of temperature can not be ignored in any attempt to model the growth of fishes.

In summary the three factors, ration, size, and temperature probably have the most influence on the growth for a given species and diet. Any attempt at modeling growth must include at least these three factors as variables in the growth function.

DEVELOPMENT OF THE GROWTH EQUATION

Energy flow principals

As pointed out by Warren (1971) the key to understanding growth of an organism is to study the energy flow or bioenergetics of the organism. Bioenergetics is the study of energy transformations in a living biological system (Lehninger, 1965). Definitions of the system may vary from one discipline to another. A biological system may be the cell to the biochemist, the individual organism to the physiologist, the population of organisms to the population dynamist or the community of populations to the ecologist. In all cases the biological systems are open to both energy gains and losses at various rates over time. Consequently the classical laws of thermodynamics of closed systems in equilibrium form the basis of thought (Lehninger, 1965). Brief accounts of the history of the application of the principal of bioenergetics to fishes are given by Warren and Davis (1967), Warren (1971), Weatherley (1972). From the laws of thermodynamics, the change in total energy content of a system balances the sum of the uses of energy by the system to perform work (Warren, 1971). In consumer organisms like fish, this means that the energy content of the food consumed over a period of time, denoted by F, must be equal to the change in energy content of the body, dW/dt, plus the energy loss in the form of wastes, $(1-\rho)F$, and the energy used to perform work, M (Warren, 1971). Winberg (1956) defines ρ as the proportion of the consumed food that is assimilated into useful energy. This implies that $(1-\rho)$ is the fraction of the food that is wasted. M is referred to as total metabolism. It follows that the rate of growth can be written in terms of energy inputs minus energy losses and use, i.e.,

$$dW/dt = F - (1-\rho)F - M \quad \text{or} \quad F - M \qquad (1)$$

This is the basis for the equation of the balanced energy budget proposed by Ivlev (1945) in which he broke up energy of metabolism into energy of primary heat, external work and internal work. Warren and Davis (1967) described the energy of metabolism as the sum of the energy of standard metabolism, energy of specific dynamic action and energy of active metabolism. They defined standard metabolism as the metabolism of unfed and resting fish, specific dynamic action as the process of digestion, assimilation and storage of consumed food stuffs and active metabolism as muscular activity over and above that of the resting animal. These definitions are more concise than those of Ivlev and are subject to less ambiguity. More important though is that they are identified with a specific action for which the expended energy can usually be measured in the laboratory. Applying this to the study of growth, Warren and Davis (1967) suggest that growth potential of an organism under a given environmental condition can best be understood by studying how environmental factors affect growth through influences on food consumption and influences on the expenditure of food energy at the various activities.

Specifically they borrow from the works of F. E. J. Fry and define "scope for growth" as the difference between the energy value of all the food an animal consumes and all other energy uses and losses identified in the energy budget equation. If the influence of environmental and behavioral factors on each of the various energy consuming activities can be determined, then the resulting growth response can be explained by this difference. This approach is very useful to understanding growth but it requires a considerable number of detailed and precise experiments to accurately quantify the relations between these factors and energy uses. Warren (1971) contends that the present knowledge of the complex relations between the environment, behavior and fates of energy is inadequate to formulate a mathematical model of "scope of growth" beyond the basic energy budget equation. Even if this is true, modelers should not be discouraged from building hypothetical models of energy flow to test the feasibility of various assumptions. Kerr (1971a,b, and c) developed models of efficiencies of food conversion using this approach. He was successful in determining that his particular hypotheses provided a feasible explanation of the relation between conversion efficiencies and food consumption.

From the basic energy budget we know that food intake is the sole energy source or driving force for growth. An alternative approach then to modeling growth is to examine the direct relation between food consumption and the resulting growth for a variety of experimental conditions. The relation between daily ration and the subsequent specific growth rate for a given size fish and set of environmental conditions is commonly curvilinear (Figure 1). GSTARVED is defined as the minimum specific growth rate for zero ration. RMAINT is the level of ration that maintains the organism at a constant weight and zero rate of growth. ROPT is defined as that level of ration for which the greatest proportion is converted into fish flesh. GOPT is the corresponding specific rate of growth. RMAX is the maximum ration an individual can consume in a unit of time. GMAX is the corresponding maximum specific growth rate. Specific growth rates are negative for zero ration and increase almost linearly to zero for the maintenance level. As rations are increased from maintenance to maximum amounts the specific growth rate increases at a decreasing rate to the maximum level. Brett, et.al. (1969) acknowledge Thompson (1941) for describing this general relation. This relation has been found by Averett (1969) for coho salmon reared in the lab; Brett, et.al. (1969) for sockeye salmon fed an Abernathy diet; Hatanaka, Kosaka, and Sato (1956) for the plaice (Limanda yokohamae) fed natural foods held in the lab; Horak (1972) for rainbow trout fed prototype commercial trout diets; Dave Leith (unpublished data) for coho salmon fed Oregon Moist Pellets (OPR); and Warren, Davis, and Doudoroff (1964) for yearling cutthroat trout (Salmo clarki) reared in aquaria.

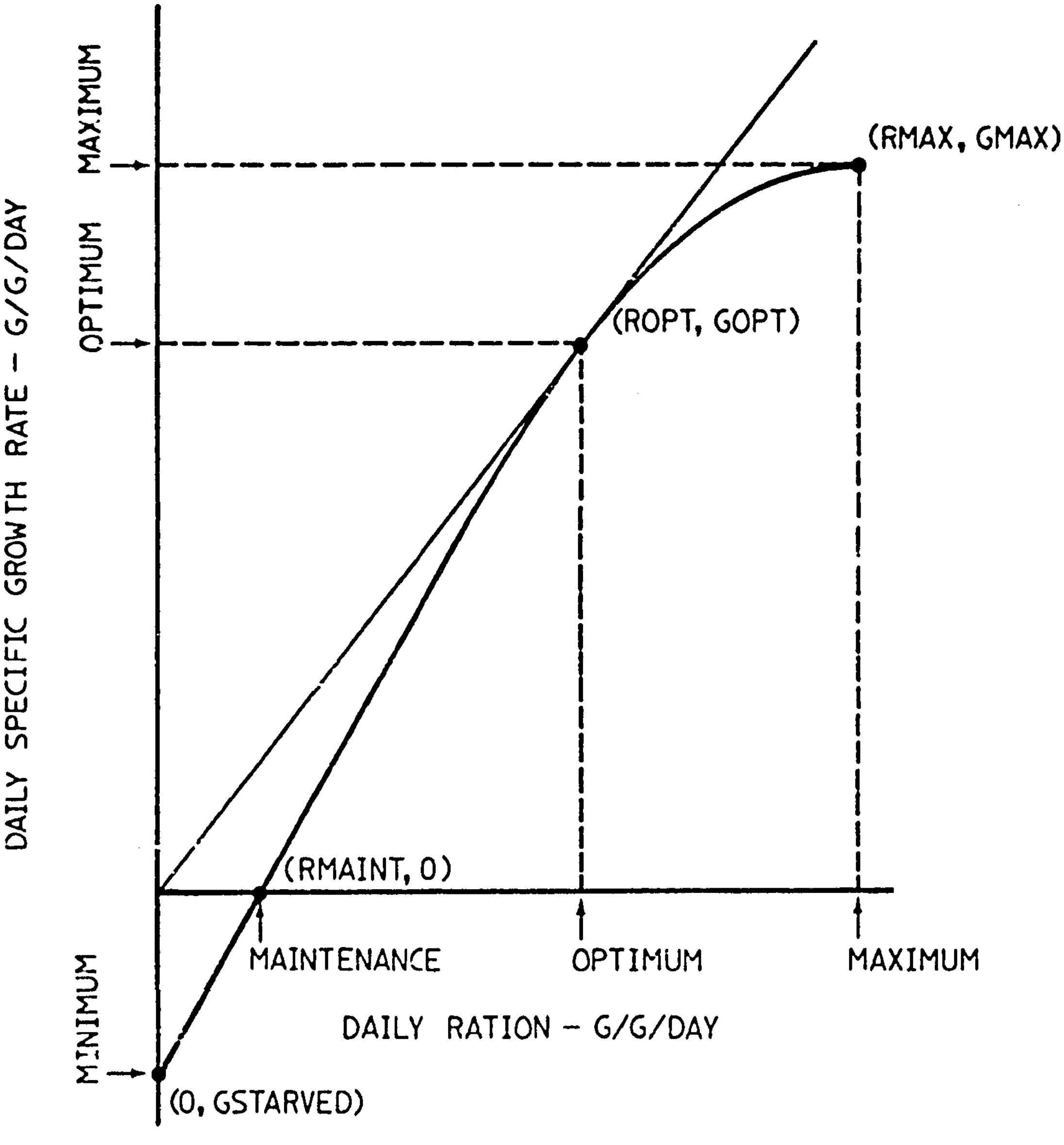


FIGURE 1. The general relationship between specific growth rate and daily ration (Brett, *et.al.*, 1969).

Dr. J. R. Brett (personal communication) now believes that the food-growth curve may be more curvilinear near starvation values. Fish acclimate to starvation or very low rations by reducing metabolism (Beamish, 1964). This would result in lower absolute values of specific growth rates for rations less than the maintenance level. The near linear relationship probably sufficiently estimates growth rates for periods of very low ration when these near starvation periods are not much longer than a week or two in duration.

These studies describe how growth varies with ration but they do not explain why. One must look to the bioenergetics of the individual fish to understand why this particular food-growth relationship occurs. Warren (1971) concludes that this curvilinear relationship is the result of the proportion of energy and materials utilized or lost in activity, specific dynamic action and waste products increasing with increasing rations. Kerr (1971a) contends that the relationship results mainly from the increasing proportion of spontaneous activity. Horak (1972) suggests that an increasing proportion of the energy intake is expended on specific dynamic action as rations increase. The difficulty in quantitativily measuring all fates of energy in one experiment results in this difference of opinion. Even though researchers do not agree on the reasons why the food-growth relationship is curvilinear, they do agree that the relationship is curvilinear as described above.

The growth model developed in this dissertation is based on this fundamental food-growth relationship. In this model ration is considered to be the sole driving force. Temperature is considered to be the major regulating force that controls the level of various rates. Weight is considered to act as a scaling factor which adjusts these rates to the size of the growing individual.

Fundamental growth equation

Ricker (1958) pointed out that any growth curve can be described adequately by the exponential growth equation,

$$W_t = W_{t_i} \exp(g_i t) \quad t_i < t < t_{i+1} \qquad (2)$$

where W_{t_i} and g_i are the same as defined earlier. That is the curve can be modeled by exponential growth for successive short stanzas. Note each interval has its own exponential growth parameter, g_i. The growth of salmonids reared in a hatchery can then be predicted by (2) as long as values of g can be estimated for each interval. The goal in this dissertation is to estimate a new g for each interval from what is known about the fish and their environment.

This goal can easily be achieved if a mathematical function can be developed that describes the specific growth rate-ration relationship in Figure 1 for all levels of the most important factors that regulate growth. There are two approaches to accomplishing this. The first is to build a data base of specific growth rates versus daily rations from all available sources of data, group the data according to environmental factors, and fit the data by response surface techniques to some appropriate function using least square techniques. The problems with this approach are: first, it is likely the data would tend to be concentrated in certain groups and not cover the range of the various environmental factors; and second, the variation in the data would probably conceal any trends in the values of the coefficients.

The second approach is to find a simple parametric function that describes specific growth rate as a function of daily ration, denoted by g(R), where the parameters are related to one or more of the biologically relevent points (0, GSTARVED), (RMAINT, 0), (ROPT, GOPT), or (RMAX, GMAX) (see Figure 1). If these points can be identified as functions of those factors considered to have the most influence on growth, then with the proper substitutions specific growth rate can be described as a function of daily ration and the identified factors. The point (ROPT, GOPT) is the most difficult to investigate and the least known since there is no easy procedure for identifying ROPT unlike the other points.

Three functions that come close to meeting these requirements are:

$Y = a + bX$	straight line
$Y = aX/(X + b)$ or $a/(1 + b/X)$	Michaelis-Menton curve
$Y = a \sin(bX + c)$	sine curve between $-\pi/4$ and $+\pi/2$

The alternative coefficients of the straight line function for g(R) equal to Y and R equal to X are

a = GSTARVED

b = |GSTARVED|/RMAINT,

(GOPT + |GSTARVED|)/ROPT,
GOPT/(ROPT - RMAINT),
GMAX/(RMAX - RMAINT), or
(GMAX + |GSTARVED|)/RMAX.

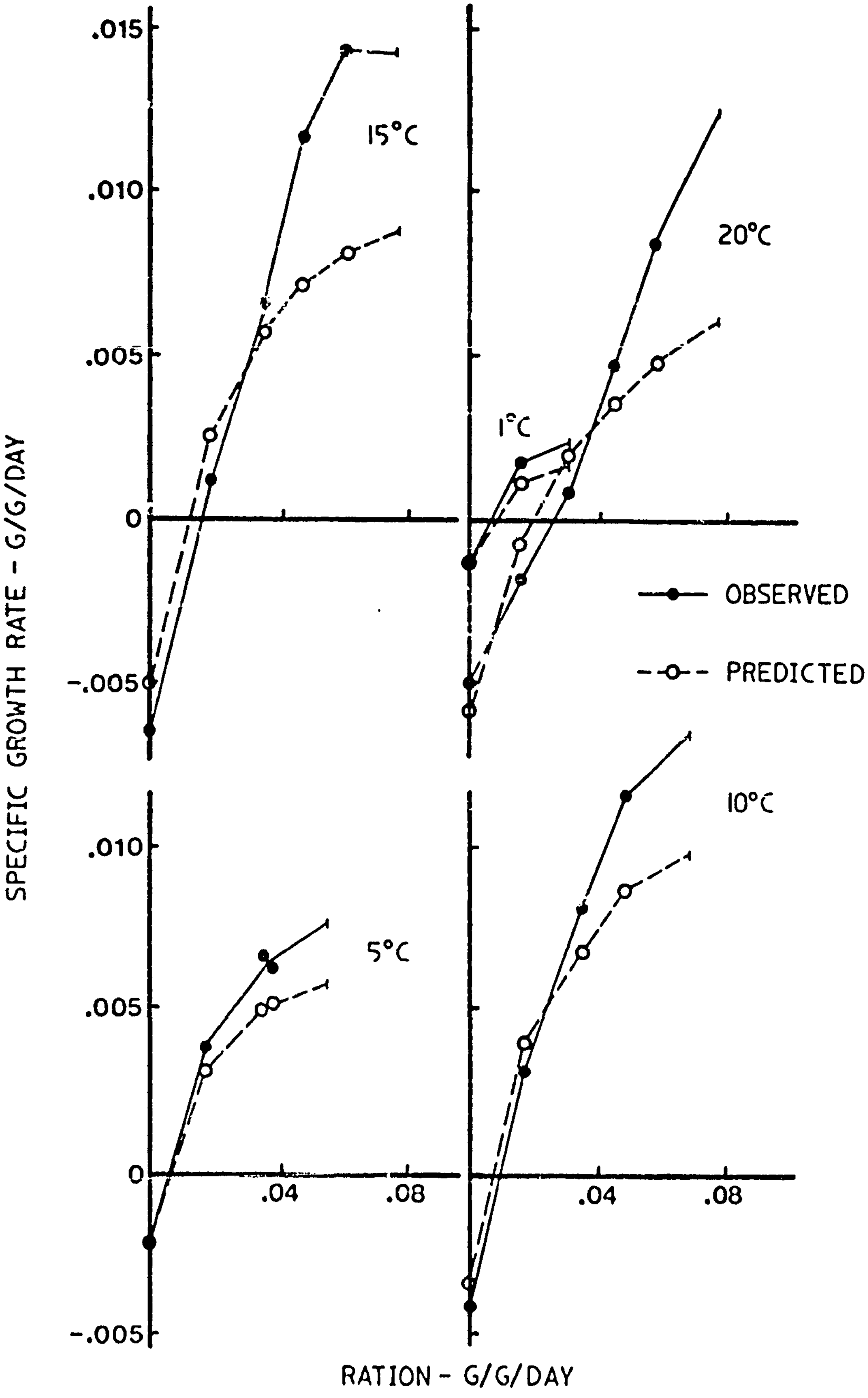
The first form of b is undesirable because it requires extrapolation for most of the range of possible rations. The second and third forms are undesirable becuase they involve the point (ROPT, GOPT), although they best describe the relation for rations less than the optimum value. The last two forms of b are the easiest to evaluate but they give the poorest description since they underestimate g everywhere except at the extremes. For these reasons the straight line function was discarded.

The Michaelis-Menton curve was adjusted to give negative growth rate values for rations less than maintenance level, i.e.,

$$g(R) = aR/(R + b) - c \quad \text{or} \quad a/(1 - b/R) - c$$

The parameter a equals GMAX + |GSTARVED| where RMAX equals infinity, b is Rb the ration that corresponds to Gb, the growth rate equal to (GMAX - |GSTARVED|)/2, and c equals |GSTARVED|. The disadvantage to this curve is that RMAX is infinite and GMAX is an asymptote. Also values of Rb like ROPT are difficult to determine. The data for growth rates versus ration given by Brett, et.al. (1969) were simulated with this curve inputting coefficient estimates taken from his empirical curves. The results of this simulation are shown in Figure 2. The curves appear adequate for rations below ROPT. Above ROPT, the Michaelis-Menton curve underestimates the value of specific growth rates. The Michaelis-Menton curve was discarded for these reasons.

FIGURE 2. Comparison of observed specific growth rates for sockeye salmon (Brett, *et.al*. 1969) with those predicted by Michaelis-Menton curve.


SPECIFIC GROWTH RATE - G/G/DAY
RATION - G/G/DAY
.015
.010
.005
0
-.005
.04
.08
15°C
20°C
1°C
5°C
10°C
OBSERVED
PREDICTED

The sine function between $-\pi/4$ and $+\pi/2$ appears to give the best geometric description of the relation of specific growth rate to daily ration. In this case the parameters are

$$a = \text{GMAX}$$

$$b = \frac{\pi}{2\ (\text{RMAX} - \text{RMAINT})}$$

$$c = \frac{\pi}{2}\left(\frac{\text{RMAINT}}{\text{RMAX} - \text{RMAINT}}\right)$$

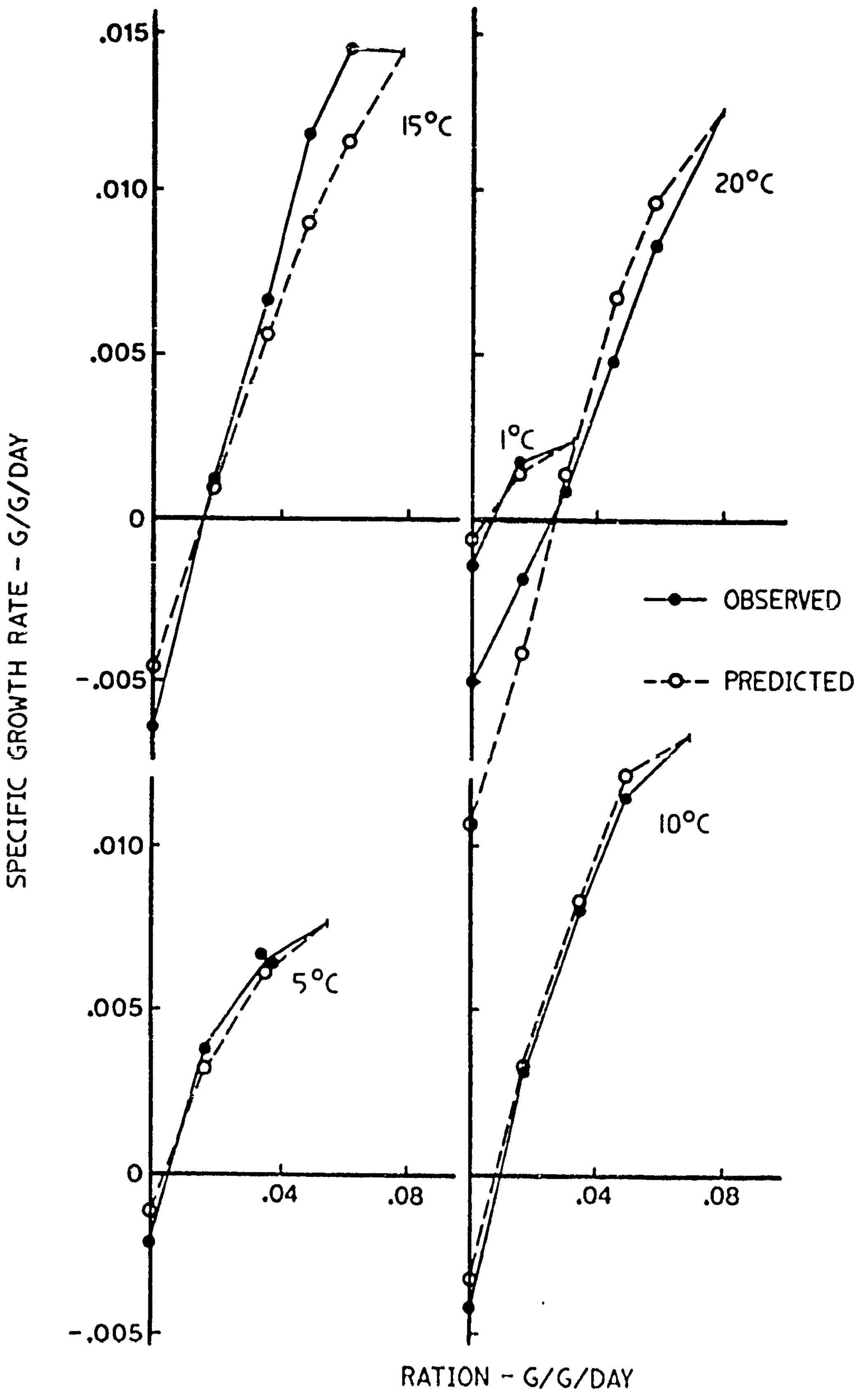
so that

$$g(R) = \text{GMAX} \bullet \text{SIN}\left(\frac{\pi}{2}\left(\frac{R - \text{RMAINT}}{\text{RMAX} - \text{RMAINT}}\right)\right) \qquad (3)$$

This expression easily accounts for the negative growth rates for rations less than the maintenance level. All the parameters are composed of biologically relevant points that can be measured in simple experiments. None of the parameters are asymptotes. The data from Brett, et.al. (1969) were also simulated using this equation (see Figure 3). In general the predicted values agree reasonably well with the observed specific growth rates at all temperatures. Although this algebric expression does not explain the growth phenomenon, it does contribute to the understanding of growth and provides an easily manipulated equation which appears to describe the locus of points in the food-growth relationship at various temperatures.

With specific growth rate expressed as a function of ration, the next step is to incorporate the other two important factors, temperature, T, and weight, W, in the growth function.

FIGURE 3. Comparison of observed specific growth rates for sockeye salmon (Brett, *et.al.* 1969) with those predicted by the sine function.


.015
.010
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0
-.005
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-.005
15°C
20°C
1°C
5°C
10°C
OBSERVED
PREDICTED
.04
.08
.04
.08
SPECIFIC GROWTH RATE - G/G/DAY
RATION - G/G/DAY

Because of the potential for a large number of coefficients in the final form of the growth model, the objective was to establish coefficients that are measurable biological quantities and to standardize the coefficients to some common temperature and fish size. If this can be accomplished then adjustment of the model to meet a new situation with different species, diets or rearing facilities should involve only a minor manipulation of coefficients. This was accomplished by treating each of the three parameters, RMAINT, RMAX, and GMAX as the product of two functions, $f_i(T)$ times $f_j(W)$, i.e.,

$$\mathrm{RMAINT} = f_1(T) \cdot f_2(W) \tag{4}$$

$$\mathrm{RMAX} = f_3(T) \cdot f_4(W) \tag{5}$$

$$\mathrm{GMAX} = f_5(T) \cdot f_6(W) \tag{6}$$

This assumes that the logarithmic transformations of the effects of temperature and weight are independent and additive. Although contradictive evidence can not be found, evidence presented later supporting these assumptions was found.

In preview of the material developed in the following sections, the weight functions $f_2(W)$, $f_4(W)$ and $f_6(W)$ are described by the equations $\ell_3 W^{-\ell_4}$, $\ell_7 W^{-\ell_8}$, and $a_6 W^{-a_7}$ respectively. The coefficient, ℓ_3, is seen to be the maintenance ration of a 1.0 gram fish. Similarily ℓ_7, is the maximum ration, and a_6 is the maximum specific growth rate. The temperature functions $f_1(T)$, $f_3(T)$, and $f_5(T)$ are various algebric expressions that essentially adjust the values of ℓ_3, ℓ_7, and ℓ_6 for changes in temperature. These functions are standardized to equal 1.0 at

10°C (50°F). To be consistent with standard hatchery records, these three temperature functions require that temperature be measured in Fahrenheit units but for the purpose of this dissertation all temperature measurements will be presented in Centigrade units with the Fahrenheit equivalent in parentheses. The coefficients ℓ_3, ℓ_7, and a_6 are measured in terms of dry weights of food and flesh to facilitate the handling of diets with different moisture contents.

The maintenance ration expression

The relation of maintenance ration to weight and temperature is best investigated from the standpoint of the balanced energy budget. For equation (1) the growth rate, dW/dt, must equal zero for maintenance rations by definition. It follows then that the assimilated portion of the food consumed at the maintenance level must equal total metabolism, *i.e.*,

$$\rho F = M \tag{7}$$

Winberg (1956) and Paloheimo and Dickie (1966) reviewed the fisheries literature and concluded that the relation between total metabolism and fish size can be described by

$$M = \alpha W^{\gamma} \tag{8}$$

Paloheimo and Dickie confirmed Winberg's conclusion that γ or the "weight exponent" is consistently around 0.8 for a variety of environmental conditions. However their examination of α revealed that it varies according to temperature and feeding levels.

If equations (7) and (8) hold true, then maintenance level of food consumption, FMAINT, can be expressed in terms of fish size with the proper substitutions, i.e.,

$$\text{FMAINT} = (\alpha/\rho)W^{\gamma} \quad \text{or} \quad \alpha' W^{\gamma} \qquad (9)$$

Beverton and Holt (1957) fit the maintenance level of food consumption of the plaice (Pleuronectes platessa) to (9) for data taken from Dawes (1930 and 1931). They estimated $\gamma = 0.665$. Dawes fed the plaice a diet of chopped mussel in pens submerged in sea water, where temperature varied naturally. Paloheimo and Dickie (1966) estimated $\gamma = 0.63 \pm 0.06$ for these same data. These latter authors also analyzed maintenance feeding levels for brown trout data taken from Pentelow (1939). Using (9) their statistical analysis yielded an estimate of $\gamma = 0.79 \pm 0.07$. Pentelow held his trout at various temperatures and fed them live gammarus (Pentelow 1939). Brown (1946b) conducted maintenance experiments on brown trout also. The trout were held at 11.5°C (52.7°F) and fed a meat diet of 77.5% moisture. These data yield an estimate of $\gamma = 0.35$ which is unusually low (Paloheimo and Dickie, 1966a). Paloheimo and Dickie (1966a) examined the relation between total metabolism and fish size for a number of sets of data taken from the literature using (8). In these cases feeding levels were generally higher than maintenance, but in most cases γ was near 0.8. From the available evidence it appears that γ is near 0.8 but may be as low as 0.667.

To convert maintenance food consumption values to maintenance rations as defined earlier, divide (9) by W, i.e.,

$$RMAINT = FMAINT/W = \alpha' W^{\gamma}/W = \alpha' W^{\gamma-1} \qquad (10)$$

The term, $\gamma-1$, then has a value ranging from -0.2 to -0.333. Although the information is not complete for hatchery salmonids, the best alternative is probably $(\gamma-1) = -0.2$. It is possible to examine the alternatives by the growth simulator at those hatcheries which feed maintenance rations at various times of the year.

Data that describe the maintenance ration - temperature relationship are given by Pentelow (1939) and Brown (1946b) for brown trout and Brett, et.al. (1969) for sockeye fingerlings. If Pentelow's data are sorted and averaged for groups to superficially remove the variability in the values, a consistent pattern develops for RMAINT versus temperature as shown in Figure 4. Generally RMAINT increases exponentially with respect to increases in water temperature. The pattern is similar for all size groups.

Brown (1946c) estimated the RMAINT (denoted by $RMAINT_{50,T}$) for a 50 gram brown trout for a wide range of temperatures, T, from a scatter of maintenance values (denoted by $RMAINT_{W,T}$) taken for various size fish at various temperatures. She assumed that maintenance ration and body weight relationship was the same at all temperatures and therefore interaction between body weight and temperature did not exist. From this basis she estimated $RMAINT_{50,T}$ for a range of temperatures in degrees centigrade by the simple proportion

$$RMAINT_{50,T} = \left(RMAINT_{50,11.5}\right)\left(RMAINT_{W,T}\right)\Big/RMAINT_{W,11.5}$$

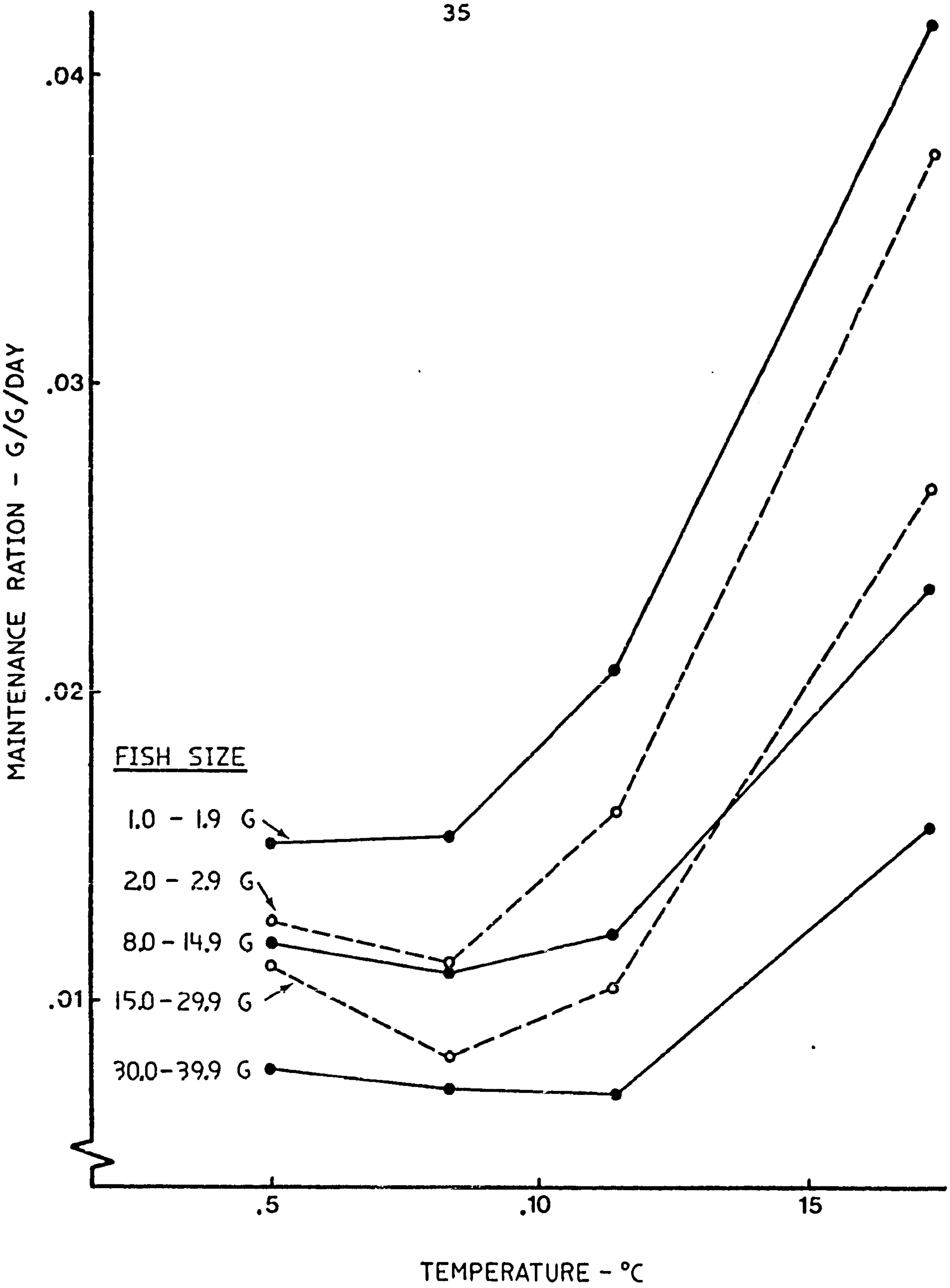


FIGURE 4. The averaged temperature relationship for the maintenance ration of five size groups of brown trout taken from Pentelow (1939).

where $RMAINT_{W,11.5°}$ are values interpolated from her RMAINT versus body weight curve (Brown, 1945b, Figure 6). This resulted in a sigmoid curve with $RMAINT_{50,T}$ increasing with increases in temperature and an inflection point occurring around 10°C (50°F).

Brett, et.al. (1969) estimated values for daily maintenance requirements of 5 to 6 gram sockeye fingerlings by interpolation of growth - ration curves. They found an exponentially increasing relationship similar to Pentelow's data.

Paloheimo and Dickie (1966) modified (9) to account for the effect of temperature on maintenance ration. They assumed that the effect of temperature is additive to the logarithmic transformation of equation (9). In a similar fashion (10) can be modified to give

$$\log_{10} RMAINT = \log_{10}\alpha' + (\alpha-1)\log_{10} W + k(T - T_s)$$

where T_s is some standard temperature, say 10°C (50°F). The antilog of this expression is

$$RMAINT = \left(\ell_1 10^{\ell_2 T}\right)\left(\ell_3 W^{-\ell_4}\right) \tag{11}$$

where $\ell_1 = 10^{-\ell_2 T_s}$, $\ell_2 = k$, $\ell_3 = \alpha'$, and $\ell_4 = -(\alpha-1)$. Equation (11) is in the desired form of (4) with

$$f_1(T) = \ell_1 10^{\ell_2 T} \quad \text{and}$$

$$f_2(W) = \ell_3 W^{-\ell_4}$$

Brett, et.al. (1969) applied this exponential form of $f_1(T)$ to their sockeye data. Changing the temperature units to Fahrenheit degrees and standardizing at 10°C (50°F), their published data give the estimate

$$f_1(T) = 0.0397 \cdot 10^{.0280T}$$

Logarithms to the base 10 as opposed to the base e are used in $f_1(T)$ in order to be consistent with the presentation of Brett, et.al. (1969). The power function, $\ell_1 T^{\ell_2}$, with temperature in Centigrade degrees also fit Brett's sockeye data, but this function does not fit his data when the temperature scale is converted to Fahrenheit.

The next step is to come up with a reasonable value for ℓ_3, the maintenance ration of a 1.0 gram fish at 10°C (50°F) on a dry weight basis. Pentelow (1939), Brown (1946b and c), Averett (1969), Brett, et.al. (1969) and Kono and Nose (1971) have published data that provide estimates of ℓ_3 by solving (11). The estimates are confounded by unknown values for the moisture content of both food and fish flesh for some of these experiments. Averett (1969) and Brett, et.al. (1969) presented their data on a dry weight basis for coho and sockeye salmon respectively. However, Pentelow fed his brown trout live gammarus, Kono and Nose fed their rainbow trout fresh anchovy larvae, and Brown fed a meat diet with 77.5% moisture to her brown trout. In these three cases it is probably safe to assume that the moisture contents of both the food and fish flesh were nearly equal. If this is true, then their values of maintenance ration are essentially unchanged by converting from a wet to a dry weight basis.

These sources provide 11 estimates of ℓ_3 by solving (11) using the observed values of RMAINT, temperature, and fish weight and setting $\ell_1 = 0.0397$, $\ell_2 = 0.0280$, and $\ell_4 = 0.2000$. The average of ten of these estimates, excluding one from Brown (1946b and c), is 0.0236 g/g/day with a 95% confidence interval of ±0.0138. The estimates of ℓ_3 are summarized in Table 1. The estimate of ℓ_3 from Brown (1946b and c) is 0.0380 g/g/day. This estimate is based on a maintenance ration of 0.02 g/g/day for a 25 gram brown trout at 10°C (50°F). Since this value is just above the upper limit and the estimate of γ from the maintenance data of Brown (1946b) was high (0.665), her estimate was discarded. The values of RMAINT for coho salmon were interpolated from the series of figures in Averett (1969) that show the relation between specific growth rate and daily ration. This method is the same Brett, et.al. (1969) used for obtaining RMAINT values for sockeye salmon. For a diet with a 32% moisture content like Oregon Moist Pellet (OPR) and for fish that average 75% moisture the wet weight value of the average 0.0236 is 0.0087 g/g/day. Based on a preliminary examination of hatchery data this appears to be reasonable.

The parameter RMAINT appears to be adequately described as a function of weight and temperature by (11) with $\ell_1 = 0.0397$, $\ell_2 = 0.0280$, $\ell_3 = 0.0236$, and $\ell_4 = 0.2000$. This submodel can be partially checked by simulating the growth of coho and spring chinook salmon at times when the fish are held on maintenance rations.

TABLE 1. Estimates of ℓ_3, maintenance ration of a 1.0 gram fish at 10°C (50°F), from various sources in the literature.

Fish Size Grams	Temperature °C(°F)	Observed RMAINT g/g/day	ℓ_3* g/g/day	Source	Species	Diet
2.1	3.3 (38)	.0117	.0300	Pentelow (1939)	brown trout	live grammarus
2.1	3.3 (38)	.0127	.0320	Pentelow (1939)	brown trout	live grammarus
2.0	7.2 (45)	.0113	.0180	Pentelow (1939)	brown trout	live grammarus
1.9	11.1 (52)	.0217	.0220	Pentelow (1939)	brown trout	live grammarus
1.2	8.0 (46.4)	.014	.0180	Averett (1969)	coho salmon	house fly larvae
1.2	11.0 (51.8)	.029	.0270	Averett (1969)	coho salmon	house fly larvae
1.9	8.0 (46.4)	.014	.0200	Averett (1969)	coho salmon	house fly larvae
1.9	11.0 (51.8)	.027	.0280	Averett (1969)	coho salmon	house fly larvae
5-6	10.0 (50.0)	.01	.0140	Brett (1969)	sockeye salmon	meal diet
7.91	12.5 (54.3)	.023	.0270	Kono & Nose (1971)	rainbow trout	fresh anchovy larvae
		mean	.0236	±0.0138 95% confidence interval		

* values were obtained by solving (11) for ℓ_3.

The maximum ration expression

Empirical derivation

The maximum amount of food a fish can consume daily must depend in some way on the physical capacity of the fish, its appetite and the digestion rate of food. A number of studies have confirmed that a definite maximum daily ration exists for a variety of species (Moore, 1941; Windell, 1966; Magnuson, 1969; Brett, 1971a; Kono and Nose, 1971). Moore (1941) noted total food consumption over one week does not vary as greatly from one week to the next as does daily consumption from day to day. Brett and Higgs (1970) noted that a large meal is often followed by a small meal and vice versa. Kono and Nose (1971) found that the total daily meal consumed by rainbow trout increased with the frequency of feeds but the maximum meal size reached in 6 feedings was not increased by 12 feedings.

The most available sources of information on the relation of daily ration with fish size and temperatures are the widely used feeding tables. These tables provide the fish culturists with a recommended feeding level for a wide range of water temperatures and fish sizes. Unfortunately the recommended feeding levels are not necessarily near the maximum. The majority of the existing tables are apparently based on the original 1952 feeding chart developed by New York State Conservation Department (EIFAC, 1971; Haskell, 1959). The exception is the new chart of maximum rations for coho salmon developed by the Fish Commission of Oregon (FCO). The Oregon chart is based on feeding experiments with coho fingerlings held for 2 or 3 weeks at constant temperatures and fed twice daily seven days per week. The chart is apparently accurate for chinook and coho, but in some cases consumption may be as much as 25% higher than the recommended values in the chart (Mr. Dave Leith, personnal communication). All the charts support the assumption that temperature and weight act independently in loglinear fashion.

Since daily ration, R, is the food consumption, F, divided by the fish weight, W, the relationship between maximum ration and weight is best examined as the food consumption-weight relationship. This eliminates any problems resulting from the correlation between 1/W and W. Brett (1971a) presents the maximum daily ration for three sizes of sockeye juveniles (5, 44, and 216 grams) held at 15°C (59°F). He found that maximum rations versus weight relationship was linearized by the logarithmic transformation, i.e.,

$$\log(\mathrm{RMAX}) = b_0 + b_1 \log(W)$$

This suggests the following expression for $f_4(W)$

$$f_4(W) = b_0' W^{b_1}$$

where $b_0' = \exp(b_0)$. Food consumption, F, in grams of food (dry weight)/day can be estimated from the weight of his sockeye fingerlings by

$$F = 0.287\ W^{0.650}$$

In terms of maximum ration on a dry weight basis in g/g/day this is

$$f_4(W) = 0.287\ W^{-0.350}$$

for 15°C (59°F). The regression of the dry weight values of the 10°C (50°F) maximum rations in the new Oregon chart gives

$$F = 0.171\ W^{0.631}$$

The conversion to dry weight was based on the 32% moisture content of the diet and an assumed moisture content of 75% for the fish flesh. Transforming this equation to maximum daily rations gives

$$f_4(W) = 0.171\ W^{-0.369}$$

Pentelow (1939) observed this general trend of decreasing maximum daily rations with increases in size for brown trout. Baldwin (1957) also documented a similar relationship for brook trout fed live minnows. The recommended feeding levels in the more popular feeding tables also decrease as fish progress to larger size groups. There is no way of knowing at this point if this relationship is best described by the above equation, but it appears from the evidence to be adequate.

The coefficient, ℓ_7, is the maximum daily ration of a 1.0 gram fish at 10°C (50°F). A value of 0.200 for ℓ_7 can be estimated for Brett's (1971a) sockeye data standardized to 10°C (50°F). The value estimated by the analysis of the new Oregon feeding chart is 0.171 after accounting for moisture content.

Another estimate of ℓ_7 can be calculated from the rainbow trout data published by Kono and Nose (1971) by using (12) to correct for temperature and size. The average trout weighing 7.88 grams initially consumed a maximum ration of 0.147 g/g/day at 12.5°C (54.3°F). At standard conditions this converts to 0.242 g/g/day using the above values for the other coefficients. The value 0.171 for ℓ_7 is probably the most appropriate for hatchery salmonids fed the standard production diets. The estimated values of ℓ_8 were 0.350 and 0.369 but for the purpose of simulation this value was arbitarily simplified to 0.3333.

It is a known fact that fish can consume more food at higher temperatures than similar sized fish at lower temperatures. This makes it necessary to adjust the weight function for temperature changes. The standard feeding tables call for increasing the feeding level at an increasing rate as temperatures go up (see Figure 5). This makes a concave upward relationship between maximum ration and temperature, if feeding tables are assumed to be near the maximum level. The Abernathy and EIFAC Table IV charts for dry diets and the original chart for the Oregon moist pellet are in this category. The exceptions are the new Oregon chart of maximum rations, which recommends a concave downward relationship, and the EIFAC Table V, which recommends increasing rations almost linearly up to 16°C (60.8°F) and then drastically decreasing rations linearly for temperatures above 16°C. Brett, et. al. (1969) extrapolated from their growth rate-ration curves to get values for RMAX for their various experimental temperatures. They came up with a

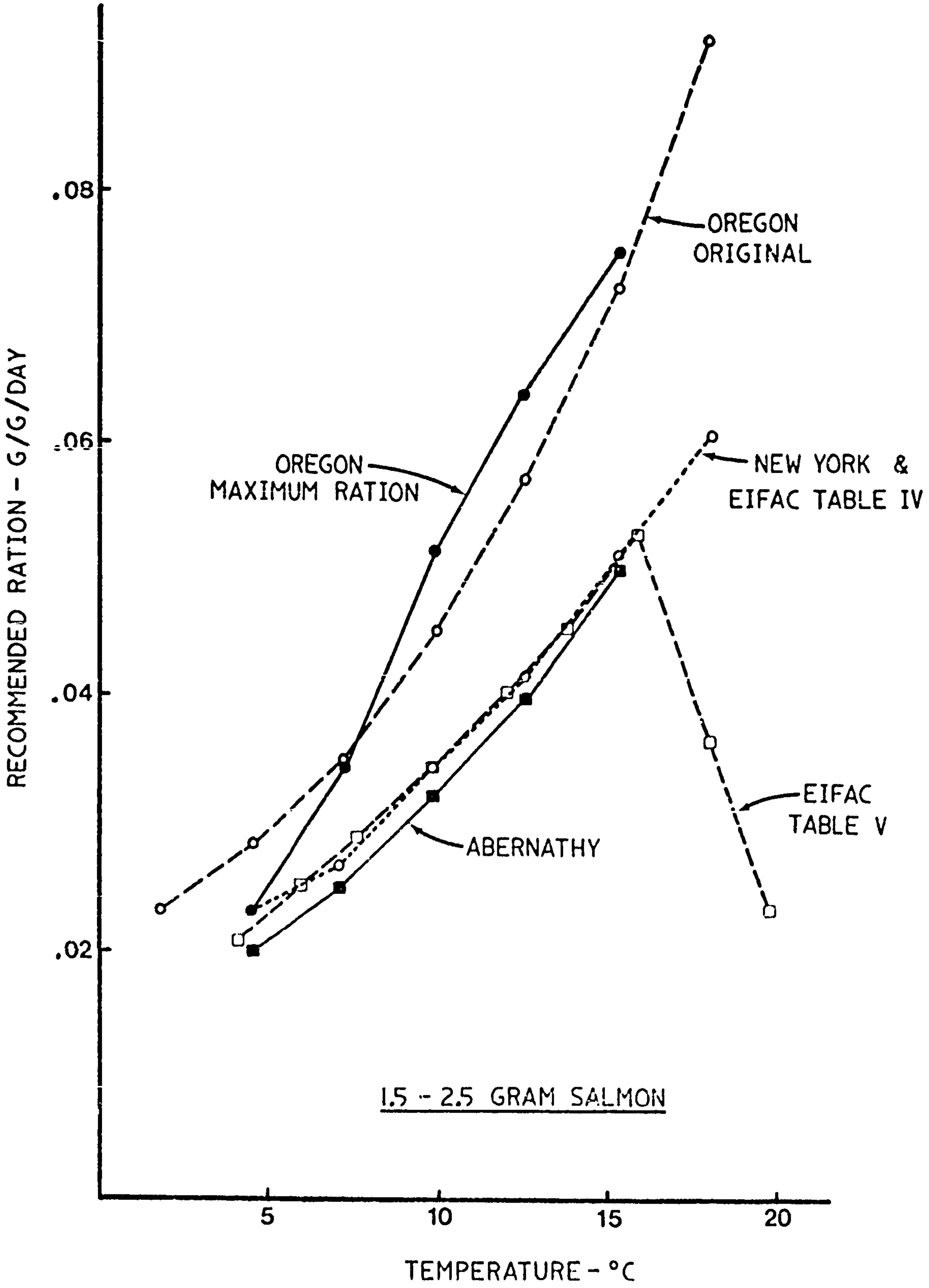


FIGURE 5. The relation between daily ration and temperature proposed by six feeding charts.

relationship similar to the new Oregon chart where maximum daily rations increased with temperature but at a decreasing rate. Their values of RMAX though are confounded with fish weight because the larger fish occurred at the higher temperatures at the end of the experiment.

The form selected for the temperature correction function, $f_3(T) = -\ell_5 + \ell_6 \log_e T$, is based on Brett, et.al. (1969) but altered to natural logarithms. Estimates of ℓ_5 and ℓ_6 were taken from the new Oregon feeding chart and standardized so that $f_3(T)$ equals 1.0 at 10°C (50°F). The values finally arrived at are $\ell_5 = 8.82$ and $\ell_6 = 2.51$. This formulation of $f_3(T)$ is totally inadequate for values very near the upper lethal temperature limit or even lower as suggested by EIFAC Table V. Apparently salmon rapidly lose their appetite 2 or 3 degrees below the lethal limit (Donaldson and Foster, 1940; Brett, et.al. (1969).

The goals initially set for the RMAX function are met by these equations for $f_3(T)$ and $f_4(W)$. Together, RMAX can be predicted for various temperatures and weights by

$$\text{RMAX} = \left(-\ell_5 + \ell_6 \log_e T\right)\left(\ell_7 W^{-\ell_8}\right) \tag{12}$$

where ℓ_7 replaces b_0' and ℓ_8 replaces $-b_1$. The values for ℓ_5 and ℓ_6 are 8.82 and 2.51 respectively. The values for ℓ_7 and ℓ_8 are 0.171 and 0.3333. The final form of (12) then is

$$\text{RMAX} = \left(-8.82 + 2.51 \log_e T\right)\left(0.171\ W^{-0.3333}\right) \tag{13}$$

where T is measured in degrees Fahrenheit, W is wet weight in grams and RMAX is the fraction of body weight consumed per day on a dry weight basis.

Theoretical investigation

In the initial stages of developing the RMAX expression, the 1971 paper by Brett and the Oregon maximum ration feeding chart were not available. The lack of information for $f_4(W)$ and the differences in the temperature relationship between sockeye data presented by Brett, *et.al*. (1969) and those suggested by the feeding table made it difficult to describe the RMAX relationships empirically. For this reason the phenonemon of RMAX was examined from the theoretical basis of the rate of food passage through the stomach. The results of this study increase the understanding of the maximum ration phenonema. They support the empirical model developed and hence are included in this dissertation.

Many investigators, examining the rate of digestion, more correctly labeled rate of gastric evacuation (Brett and Higgs, 1970; Elliott, 1972; Tyler, 1970), have found for a variety of fish species that the rate of gastric evacuation, dS/dt is proportional to the amount of food contained in the stomach, S, at any time, t, *i.e.*,

$$dS/dt = -rS_t \tag{14}$$

where dS/dt is measured in grams of food/unit of time

S_t is grams of food in the stomach at time t

r is exponential rate of gastric evacuation.

The rate of gastric evacuation includes the removal of food from the stomach by absorption through the stomach wall and passage to the intestine by peristalsis.

If (14) is true, then the amount of food, S_t, remaining in the stomach at any time, t, after a single feeding of food, S_0, is described by

$$S_t = S_0 \exp(-rt) \tag{15}$$

which is obtained by integrating (14). Estimates of r can be found by

$$\hat{r} = \left(\log_e S_t - \log_e S_0\right) / \left(-t\right) \tag{16}$$

Tyler (1970), Brett and Higgs, (1970), and Elliott, (1972) fit (15) to their respective data for cod (Gadus morhua) fed a meal of shrimp tails, for sockeye fed a moist "1/8" Abernathy pellet, and for brown trout fed a variety of natural invertebrates. Published results for a variety of other fish are characteristic of this curvilinear relationship suggested by (15) although no curve fitting was actually attempted (Kitchell and Windell, 1968; Magnuson, 1969; Seaburg and Moyle, 1964; Shirahata, 1967; Shrable, Tiemeier and Deyoe, 1969; Windell, 1966; Windell, 1967; Windell, Norris, Kitchell, and Norris, 1969). In all these cases the ration consisted of many small particles ranging from insect larvae to whole minnows to pelletized trout meal. In studies by Pandian (1967) for Megalops cyprinoides and Ophiocephalus striatus and Hunt (1960) for the Florida gar (Lepisosteus platyrhincus), warmouth (Chaenobryttus gulosus) and largemouth bass (Micropterus salmoides) evacuation of stomach contents did not follow the relationship described by (15). In both cases the test fish were fed single minnows nearly equal to stomach capacity. In these cases evacuation of stomach contents was negligible for the first few hours after which the rate of evacuation was nearly constant rather than proportional to the stomach contents. Windell (1966) observed a constant rate of evacuation for bluegill sunfish (Lepomis macrochirus) fed a meal of 4 or 5 meal worms. On the other hand, he observed this characteristic curvilinear relationship for sunfish fed a mixture of other natural diet organisms. If the diet consists of many small particles that can easily be mixed then it appears that the stomach can mix the particules with the digestive enzymes and pump the food particles into the intestine at a rate proportional to the amount remaining in the stomach. If this is true, then the absolute value of rate of gastric evacuation is maximum when the stomach is satiated, denoted by S_{max}, i.e.,

$$\max|dS/dt| = |-rS_{max}|$$

The maximum daily food consumption denoted by F_{max} is achieved when the rate of food consumption, dF/dt equals the absolute value of the maximum rate of gastric evacuation (Tyler, 1970), i.e.,

$$\max(dF/dt) = \max|dS/dt| = rS_{max}$$

This assumes that a fishes' appetite during satiation, even though it is low (Magnuson, 1969; Brett, 1971a) is enough to maintain consumption of food at a rate equal to the rate of gastric evacuation. If this is true, then the maximum daily food consumption is equal to the sum of the initial meal, F_0, and the integral of max(dF/dt) with respect to the feeding time interval, *i.e.*,

$$F_{max} = F_0 + \int_{t_s}^{t_e} \max\left(\frac{dF}{d\tau}\right) d\tau$$

$$= F_0 + \int_{t_s}^{t_e} rS_{max}\, d\tau$$

$$= F_0 + rS_{max}\,(t_e - t_s)$$

where t_s is time feeding starts, and

t_e is time feeding ends

$$= F_0 + rS_{max}\Delta t_f \qquad (17)$$

where Δt_f is feeding time interval, $(t_e - t_s)$. The initial meal size F_0 is approximately the difference between maximum stomach capacity, S_{max}, and the remaining stomach contents from the previous meal (Windell, 1966; Brett, 1971a; Brett and Higgs, 1970), *i.e.*,

$$F_0 = S_{max} - S_{max}\exp\left(-r\left(t_s - t_{ep}\right)\right)$$

where t_{ep} is time feeding ended for the previous meal

$$= S_{max}\left(1 - \exp\left(-r\Delta t_n\right)\right)$$

where Δt_n is non-feeding time interval. Substituting this for F_0 in (17) gives

$$F_{max} = S_{max}\left(1 - \exp\left(-r\Delta t_n\right) + r\Delta t_f\right) \qquad (18)$$

The maximum amount of food consumed during a feeding period is the accumulation of the initial meal plus the steady comsumption thereafter until the end of the feeding for the day.

The feeding experiments on skipjack tuna (*Euthynnus pelamis*) conducted by Magnuson (1969) support the model. The results of this work are reproduced in Figure 6. Magnuson fed white bait every 15 minutes for 3 consecutive days to three groups of skipjack tuna, 44 cm in length and 1.6 kg in weight. Each time one white bait was offered and, if it was eaten, additional white bait was offered almost immediately. The running totals of the consumed food were cumulated for quantities of food eaten at each 15 minute feeding. Magnuson (1969) noted that the results were similar for the three test days for the fish in the same group. On the other hand, the results differed greatly between groups. Group I essentially fed in the morning and afternoon, Group II ate a large meal in early morning and then continuously all day long, and Group III accepted food only in the first few hours of feeding. As the model predicts Group II consumed the highest daily total of food. Magnuson (1969) concluded that maximum stomach capacity was 100-130 grams of whitebait and maximum amount of food consumed per day was 360 grams for a 12 hour feeding interval. Two hours were required to achieve satiation for the first meal, effectively reducing

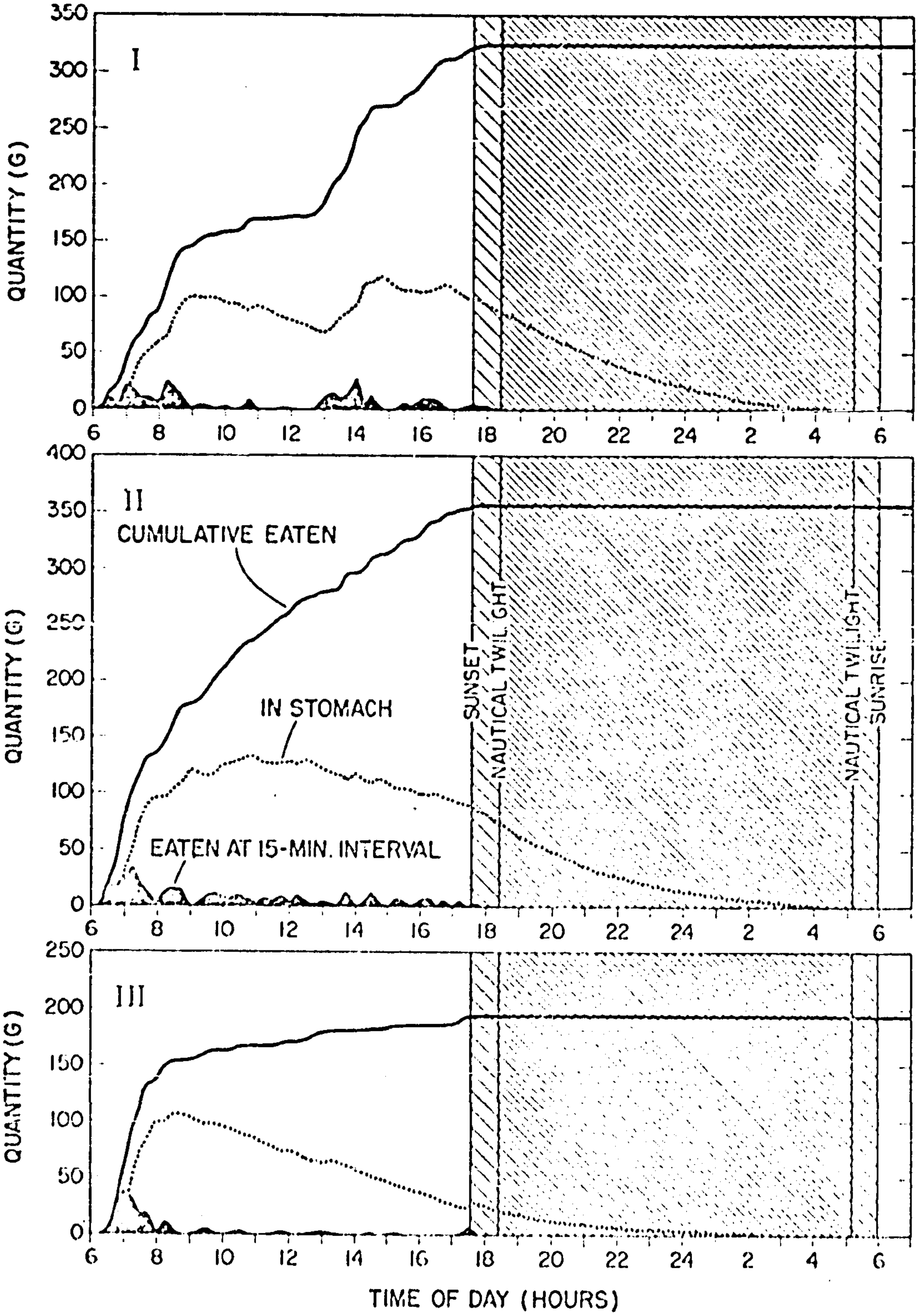


FIGURE 6. The weight of the food eaten at 15 minute intervals, the estimated weight of food in the stomach, and the cumulative weight eaten for the day for skipjack tune (Figure 5 of Magnuson, 1969).

the subsequent feed interval to 10 hours. For similar experimental conditions Magnuson (1969) measured gastric evacuation. Although he did not fit his data to (15), approximate values for r are 0.25 for the observed wet weight measurements of gastric content (uncorrected scale) and 0.20 for dry weight measurement.

Inserting the average of these values into model (18) where the stomach is assumed to be empty prior to feeding and Δt_f is 10 hours,

$$F_{max} = 115(1 + 0.225 \bullet 10) = 374 \text{ grams}$$

This value agrees very closely with the actual value of 360 grams. Although the evidence is not conclusive to prove the model, it is useable as a tool for predicting the maximum cumulative amount of food consumed per day given estimates of S_0 and r.

If feeding is assumed to be continuous over the entire 24 hour day so that the stomach is always filled to capacity, equation (18) can be simplified to

$$F_{max} = r \bullet S_{max}$$

where r is scaled in units of 1 day. From this it is easy to verify the form of the RMAX function if the relationships of S_{max} and r for weight and temperature are described in the literature.

The change in maximum food intake for a single meal with increases in fish weight for salmonids has been documented by Ishiwata (V, 1968), and Brett (1971a). Ishiwata found that satiation measured in grams of food increased linearly with increase in fish weight. He found this relationship for rainbow trout, and two species of mackerel. He measured satiation for 50 trout ranging from 3.3 to 246.8 grams at 10.9°C (51.6°F). Brett (1971a) reported that satiation measured in grams of food per body weight decreased linearly for increase in the logarithm of fish weight for sockeye fingerling ranging from 2 to 350 gram at 15°C (59°F). If the relationship for rainbow trout is transformed relative to body weight then the two give similar results. The equations are different, but they describe similar curves (Freese, 1964), i.e., grams of food per body weight decreases at a decreasing rate with increases in fish weight, approaching an asymptote near zero for large fish. This agrees with the statement by Brown (1957) that for trout the amount of food eaten per gram of fish decreases as fish grow older and larger. Pandian (1967) and (1970) fed the tropical fish M. cyprinoides and O. striatus and the dab Limanda limanda until satiation once a day with a general size range of 5-150 grams. His results agree with the above in that the amount of food consumed per day per unit of body weight on the average decreased as fish size increased. It should be noted though that the amount required for satiation depends on the type of diet. Ishiwata (1968b) observed that rainbow trout fed to satiation on a compound food accept trout eggs but not additional compound food. Therefore changing diets as fish increase size may significantly alter the growth response of the fish.

Temperature apparently has little effect on maximum meal size except near the two extremes. Low temperatures have less of an affect on maximum meal size than temperatures near the upper lethal limit. Brett and Higgs (1970) reported that maximum meal size for sockeye fingerlings was depressed at both low and high temperatures. They did find though that similar fish would ingest a meal at low temperatures in the winter equal in size to that at intermediate temperatures. The stomachs of brook trout taken from a stream during cold winter months by Leonard (1942) were well-filled, which indicated no loss of appetite. McCormack (1962) similarly noted that all trout sampled in a brook with water temperatures ranging from 1 to 2.5°C had been feeding, and most had full stomachs. Reimers (1957) noted that most trout eagerly feed even at near freezing water temperatures. Apparently, feeding behavior is inhibited by high temperature near the lethal limit. Donaldson and Foster (1940) noted that sockeye fry refused to eat in water temperatures near 25.6°C (78°F). Brett, et.al. (1969) also noted that sockeye fingerlings stopped accepting food at 24°C (75.2°F). Tyler (1970) noted that his cod would not feed at 21°C (69.8°F). Although the data are sketchy, maximum meal size appears to be relatively unaffected by temperature except for temperatures approaching the upper lethal limit when feeding ceases.

The relation between body weight and gastric evacuation has received minor attention in the literature. J. T. Windell (personal communication) is convinced that digestion rates decrease at a decreasing rate with increases in weight for trout. It is his experience that differences are greatest for 0 to 25 gram fish and rather uniformly lower for 25-150 gram range. Pandian (1967) observed differences in the times for complete stomach evacuation between four size groups of M. cyprinoides held at 28°C (82.4°F). Among the four groups 5.1 grams, 21.2 grams, 51.3 grams, and 90.6 grams, the times were 6.5 hours, 13 hours, 17 hours, and 20.5 hours. The relation between the amount of food remaining in the gut and elapsed time for Pandian's study do not fit the exponential model of gastric evacuation. If overall values of r are estimated from these data using equation (16), the estimates would decrease at a decreasing rate with increases in fish weight. A high value of r for larval fish is indicated by Rosenthal and Hempel (1970) who reported times of 4 to 10 hours for passage of food through the full length of the gut of larval herring (Clupea harengus). On the other hand, Tyler (1970) and Elliott (1972) could not detect any significant changes in r with body weight for cod (size range, 150 to 375 grams) or brown trout (size range, 82 to 358 grams). In both of these studies the factor of fish weight was of secondary importance in the experimental design. Hunt (1960) could not detect any difference in the Florida gar. Evidence from Windell (1966) also supports the conclusion that r does not vary with size. Similar values of r can be calculated for his two size groups, 33.0 and 145.4 grams, of bluegill sunfish held at 21.5°C (70.7°F).

If Windell's observation is correct, then this explains why Tyler (1970), Elliott (1972), and Windell (1966) did not find differences in digestion within larger size fish.

The conclusion from the available evidence is that exponential rates of gastric evacuation are greater for larval and fry stages than for juvenile and adult stages and that the values remain relatively constant for the larger size categories. This has not been completely confirmed for salmonid species. This relation is similar to the relation of maximum meal size with fish weight.

The influence of temperature on gastric evacuation has been thoroughly examined for many species (Brett and Higgs, 1970; Elliott, 1972; Molnár and Tölg, 1962; Molnár, Tamassy, and Tölg, 1967; Shrable, Tiemeier and Deyoe, 1969; Tyler, 1970). The data in Figure 7 shows a sigmoid relation, with r increasing at an increasing rate up to some intermediate temperature then increasing at a decreasing rate up to the higher temperature near the upper bound. In the case of cod (Tyler, 1970) gastric evacuation reached a maximum rate at 15°C (50°F) and actually decreased for higher temperatures. Measurements of gastric evacuation for catfish (Shrable, <u>et</u>.<u>al</u>. 1969) exhibited this same relation.

Rates of gastric evacuation have been shown to depend on the type of diet (Elliott, 1972; Brett and Higgs, 1970). Fats in general require more time to digest than carbohydrates and proteins (Windell, 1966). Changes in diet are likely to

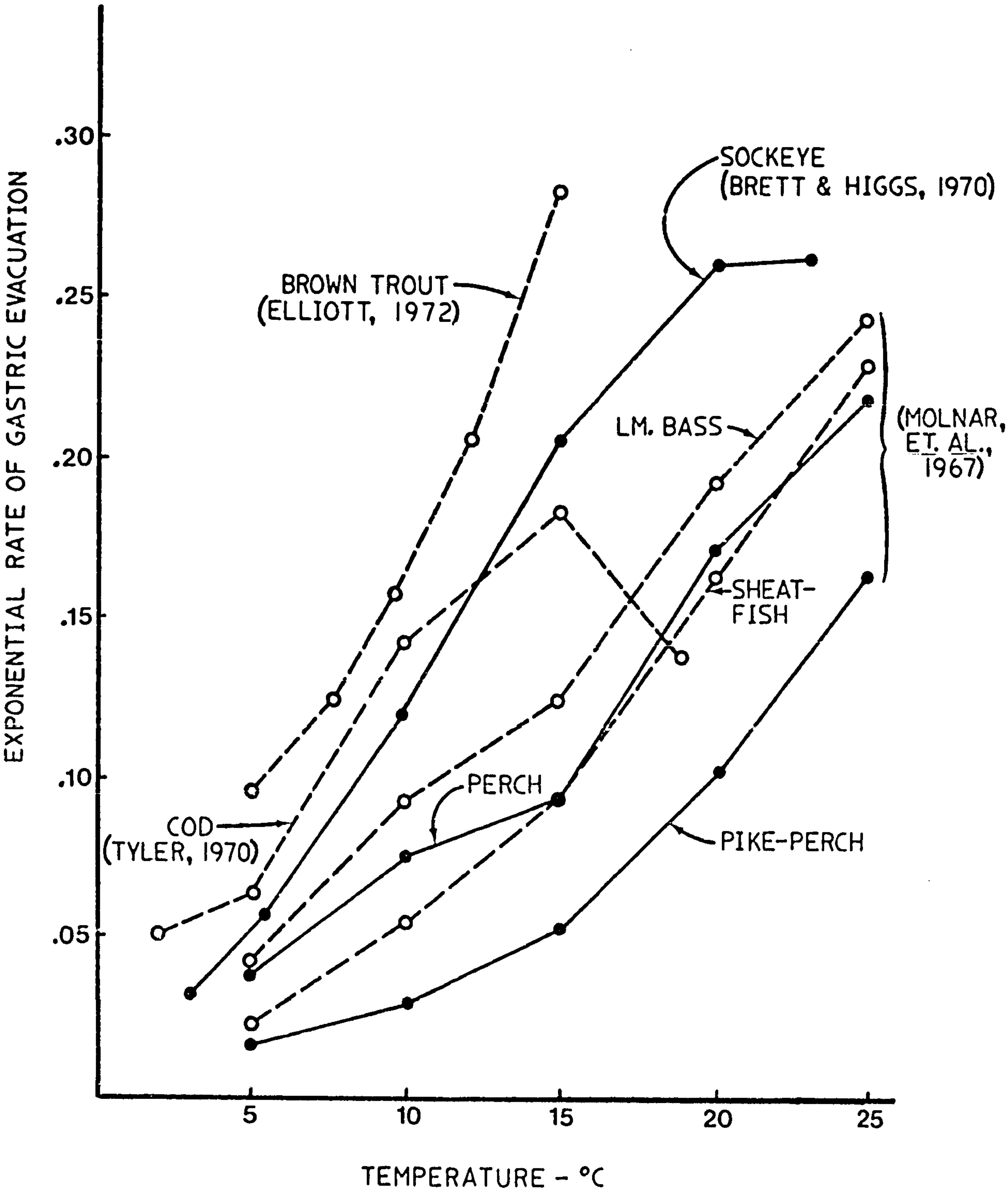


FIGURE 7. The relation between instantenous rate of gastric evacuation and water temperature for six species taken from Brett and Higgs (1970); Elliott (1972); Molnár, et.al. (1967); Tyler (1970). Gastric evacuation was assumed to be 99% complete for the data given by Molnár, et.al., (1967).

cause some differences in rates of gastric evacuation and therefore maximum daily ration.

The trends in r and S_0 with respect to temperature and fish size support the relation of RMAX with temperature and weight as proposed by (12) and (13). In the case of fish size, the influence of weight on both r and S_0 is similar to the power function used to adjust RMAX for changes in weight. The exact algebraic expression and coefficient values are not confirmed but the trend of RMAX decreasing at a decreasing rate with increases in fish weight is confirmed. In the case of water temperature, the trends in both r and S_{max} combined behave similarly to the function used to adjust RMAX for changes in temperature. For low and intermediate temperatures, RMAX is controlled mainly by rate of gastric evacuation. For low temperatures the concave upward trend in r is opposed by the concave downward trend in S_{max}. This results in the near linear relation between RMAX and temperature. For intermediate temperatures where S_{max} remains constant, both r and RMAX increase at a decreasing rate. In this extreme high temperature range, RMAX is controlled mainly by the loss of appetite and the rapid reduction in S_{max} with increases in temperature. The r value remains relatively constant or slightly decreases. This supports the temperature relationship described by $f_3(T)$ and proposed by Brett, et.al. (1969) and the new Oregon feeding chart as opposed to the concave upward curve suggested by the other standard charts. As before, the exact algebraic expression and coefficient values are not confirmed but the pattern for RMAX within the viable temperature range is confirmed.

The maximum specific growth rate expression

Fish culturists for years have been interested in measuring the maximum growth that salmonid species can achieve in hatchery environments. Haskell (1959) reviewed an equation that he developed to predict the size of trout reared in constant water temperatures and fed *ab libitum* rations. For this set of conditions, Haskell empirically determined that the length of trout, ℓ_t, beginning at some initial size, ℓ_0, increases linearly with time, *i.e.*,

$$\ell_t = \ell_0 + C(T)t$$

where C(T), the slope coefficient, is a function of temperature. If growth is isometric, *i.e.*,

$$W = k\ \ell^3$$

then the cube root of weight should increase in a similar fashion, *i.e.*,

$$W_t^{1/3} = W_0^{1/3} + C(T)t \tag{19}$$

As a result of Haskell's work, growth in trout hatcheries is commonly measured in units of inches per month.

The basis for the relation of maximum specific growth rate with temperature and fish size is developed from an analytical examination of (19). If (19) is generalized to the following

$$W_t^{1-b} = W_0^{1-b} + a(T)(1-b)t \tag{20}$$

where $1-b = 1/3$ and $a(T) = C(T)/(1-b)$, then specific growth rate, dW/Wdt, for maximum growth can be derived by differentiating (20) with respect to time. The derivation is

$$d(W^{1-b})/dt = d\left(W_0^{1-b} + a(T)(1-b)t\right)/dt$$

$$(1-b)W^{-b}dW = 0 + a(T)(1-b)dt$$

$$dW/dt \quad = a(T)W^b \tag{21}$$

and dividing both sides by W to get (21) in terms of specific growth rate

$$dW/Wdt = a(T)W^{b-1}$$

For $b = 2/3$ this is

$$dW/Wdt = a(T)W^{-1/3} \tag{22}$$

The function a(T) can be interpreted as the maximum specific growth rate of a 1.0 gram fish held at T temperature. Equation (22) can be standardized at 10°C (50°F) and split into $f_5(T)$ and $f_6(W)$ by multipling by $a(10°)/a(10°)$ where $a(10°)$ is the maximum specific growth rate for a 1 gram fish at 10°C. This looks like

$$dW/Wdt = \left(a(T)/a(10°)\right)\left(a(10°)W^{-1/3}\right)$$

thus

$$f_5(T) = a(T)/a(10°)$$

$$f_6(W) = a(10°)W^{-1/3}$$

Two growth experiments conducted at the Abernathy Salmon Culture Laboratory provide the information needed to verify $f_6(W)$ and develop $f_5(T)$. In the first experiment Banks (1971) reared chinook alevins at four constant temperatures, 7.2, 10.0, 12.8, and 15.6°C (45, 50, 55, and 60°F). The fish were fed excess rations of Abernathy dry diet for 10 weeks. Banks fitted the growth of each temperature group to (20). The estimates of C(T) and a(T) for these data are listed in Table 2. In the second experiment chinook fingerlings of five initial sizes were reared at four constant temperatures for 1 month (Banks, Fowler, and Elliott, 1971). In Figure 8 the growth rates in grams per day for these data estimated by (21) with $b = 2/3$ are compared with those calculated by the first derivative of (2), i.e.,

$$dW/dt = gW \tag{23}$$

where g is estimated by

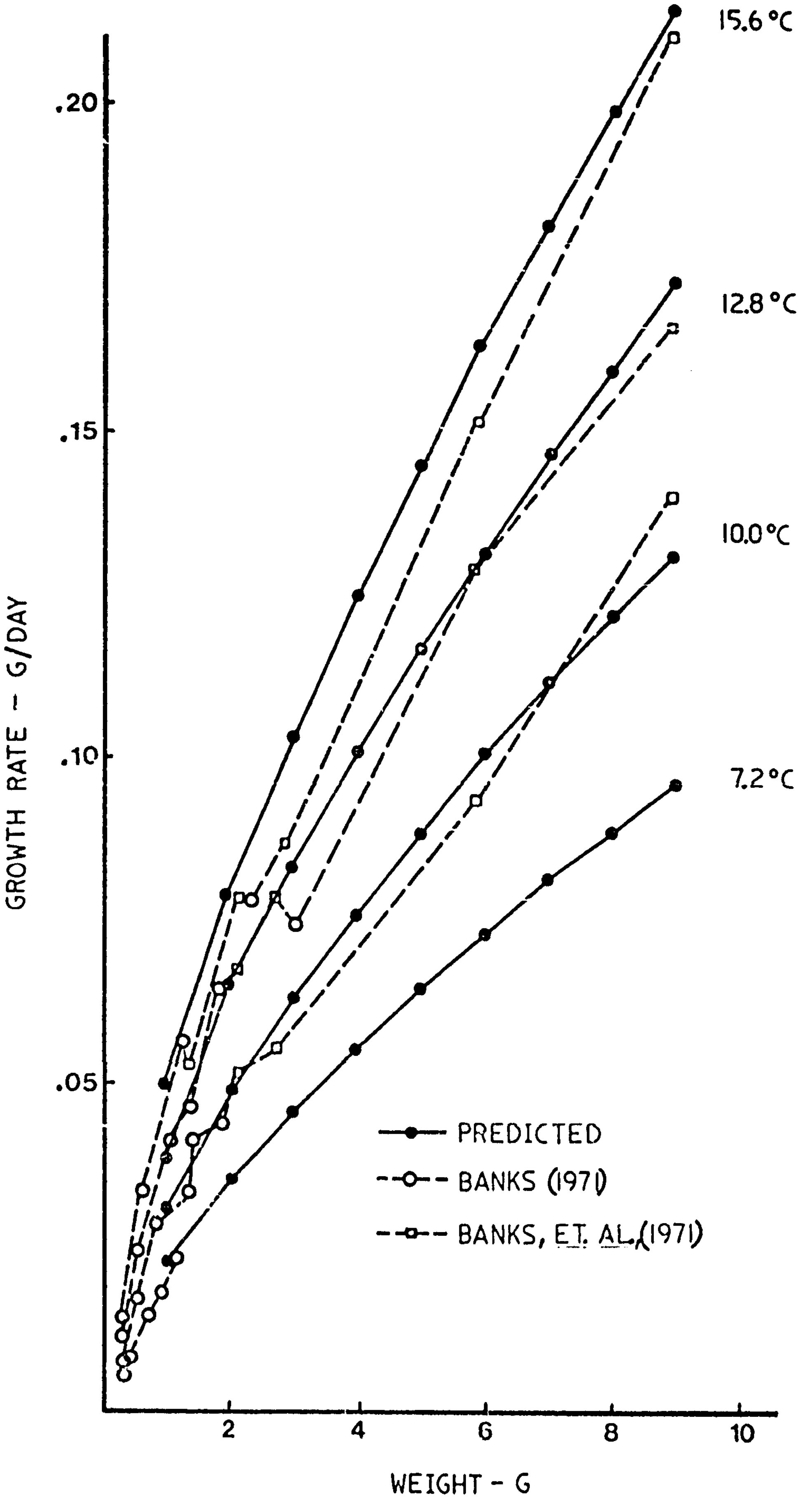
$$g = (\log_e W_t - \log_e W_0)/t \tag{24}$$

The growth rates estimated by (21) simulate values calculated by (23) reasonably well. Significant discrepancies are brought out more clearly in the comparison of specific growth

TABLE 2. Estimates of C(T) from Banks (1971), a(T), a(T)/a(10°), and the corresponding values predicted by $f_5(T)$.

Temperature	C(T)	a(T)	a(T)/a(10°)	$f_5(T)$
7.2°C	.00734	.0221	.727	.709
10.0°C	.01013	.0304	1.000	1.005
12.8°C	.01325	.0398	1.310	1.298
15.6°C	.11561	.0469	1.542	1.500

FIGURE 8. Growth rates calculated by (23) and predicted by (21) for chinook fingerlings fed excess rations at constant temperatures for two experiments conducted by Banks (1971) and Banks, *et.al.* (1971).

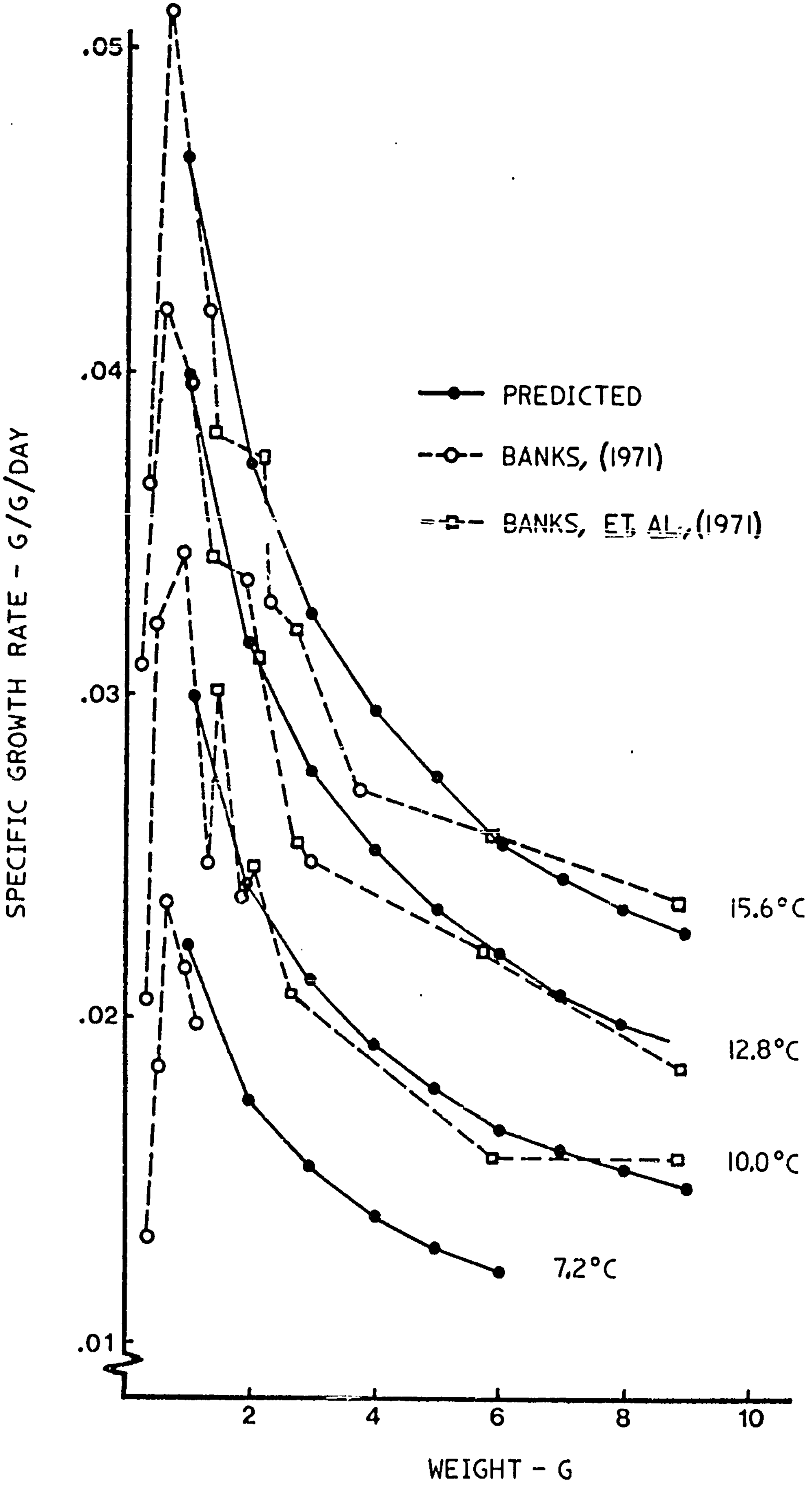

15.6 °C
12.8 °C
10.0 °C
7.2 °C
.20
.15
.10
.05
GROWTH RATE - G/DAY
2
4
6
8
10
WEIGHT - G
PREDICTED
BANKS (1971)
BANKS, ET. AL.(1971)

rates shown in Figure 9. The specific growth rates were estimated by (22) and (24). The values predicted by (22) agree closely with those estimated by (24) everywhere except for fish less than about 0.6 grams. Fish below this size are still receiving nourishment from yolk. Equation (22) is not intended to predict in this life stanza.

Brett, et.al. (1969) described the relation between specific growth rate and temperature as a dome shaped curve for juvenile sockeye fed ab libitum rations. They found that growth rate increased from near zero values for very low temperatures almost linearly to a plateau of maximum values around 15°C (59°F). For temperatures greater than 15°C, specific growth rates decreased at an increasing rate to near zero values at 24°C (73.4°F). For the temperature-specific growth rate relationship, a curve was drawn through the a(T)/a(10°) values estimated from Banks (1971) and extended beyond to the extreme temperatures by extrapolation based on Brett's sockeye information (Figure 10). This curve was fitted with a fourth degree polynomial using the regression program BMD05R (Dixon, 1965). A third degree polynomial fits equally as well except for temperatures above 20°C (68°F) where the predicted curve swings upward. The equation is

$$f_5(T) = a_1 + a_2T + a_3T^2 + a_4T^3 + a_5T^4 \qquad (25)$$

FIGURE 9. Specific growth rates calculated by (24) and predicted by (22) for chinook fingerlings fed excess rations at constant temperatures for two experiments conducted by Banks (1971) and Banks, *et.al.* (1971).


SPECIFIC GROWTH RATE - G/G/DAY
.05
.04
.03
.02
.01
2
4
6
8
10
WEIGHT - G
PREDICTED
BANKS, (1971)
BANKS, ET AL., (1971)
15.6°C
12.8°C
10.0°C
7.2°C

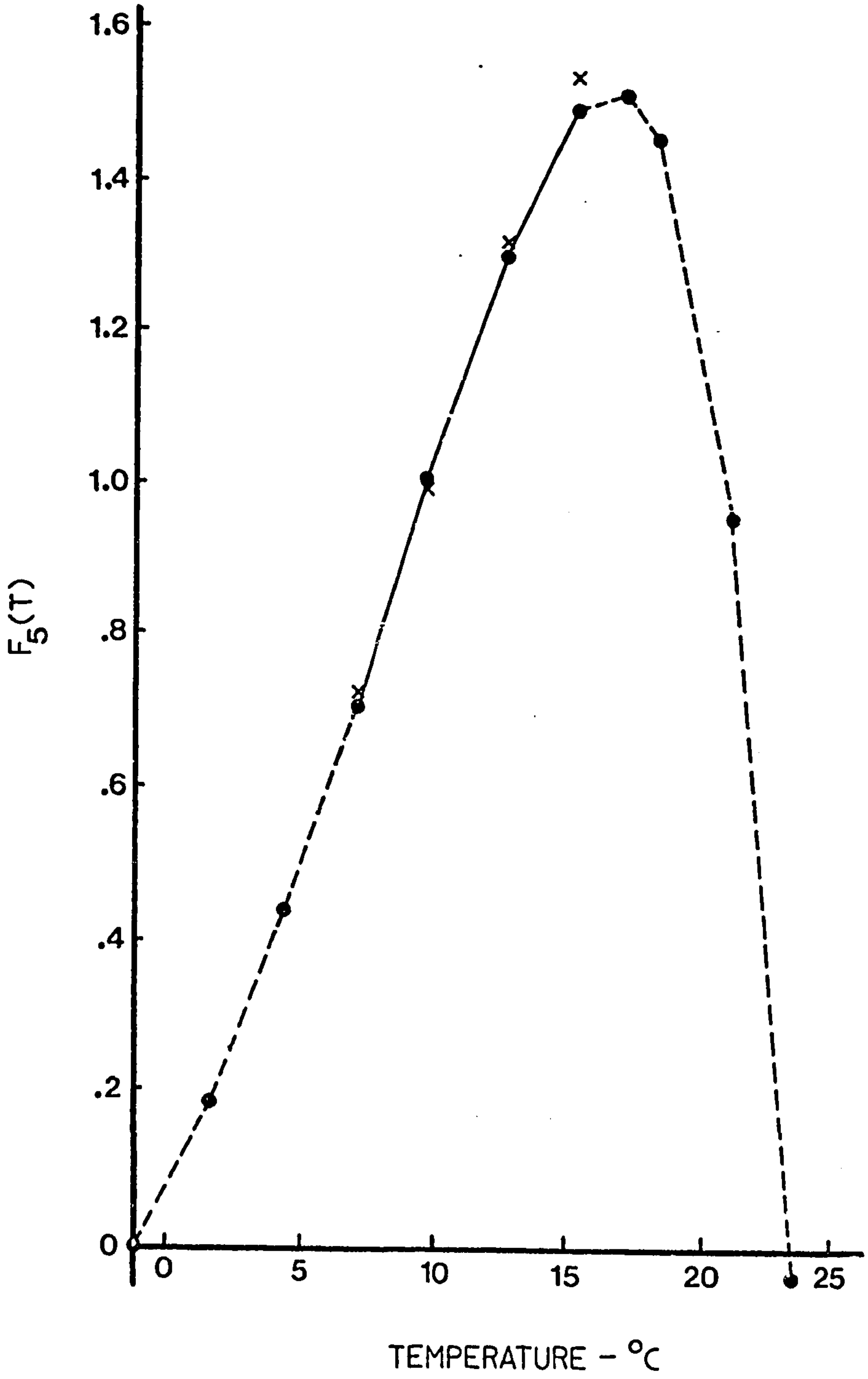


FIGURE 10. The curve of $f_5(T)$, the relation between temperature and maximum specific growth rate for the viable temperature range standardized at 10°C (50°F). The points indicated by × are derived from Banks (1971). The dashed line indicates extrapolated region based on the work of Brett, et.al. (1969).

where

$$a_1 = -15.949, \qquad a_4 = 0.00069698$$
$$a_2 = 1.3849, \qquad a_5 = -0.0000038991.$$
$$a_3 = -0.046018,$$

The function $f_6(W)$ can be rewritten in terms of a_i coefficients, i.e.,

$$f_6(W) = a_6 W^{-a_7} \tag{26}$$

where $a_6 = a(10°)$, and $a_7 = 1/3$. The estimate of a_6 from Banks (1971) is 0.0304 g/g/day. A value for a_6 equal to 0.055 was estimated from Kono and Nose (1971) rainbow trout data by solving for a_6 in (26) and correcting for temperature. Similarly a value of 0.027 was calculated from the 10°C sockeye data presented by Brett, et.al. (1969). The value from Banks (1971) was chosen as a starting value so that

$$f_6(W) = 0.0304W^{-0.3333}$$

The shape of the $f_5(T)$ curve can be explained somewhat by the portion of the daily food consumption that is available for growth. This portion is approximately the difference between the daily ration and the maintenance ration. From the definition of net efficiency of conversion, E_n, specific growth rate is equal to the product of net efficiency and this difference. At maximum ration then the corresponding specific rates of growth are

$$GMAX = E_n(RMAX - RMAINT) \qquad (27)$$

Preliminary examination of this expression for a 1.0 gram salmon using (11) and (12) reveals that GMAX values should increase almost linearly from 0°C to the maximum plateau near 15° as indicated by Brett, et.al. (1969) (see Figure 11); at these optimal temperatures metabolic costs are increasing rapidly, reducing the portion of food available for growth. The slowly increasing maximum ration resulting from nearly constant rates of digestion is not sufficient to compensate for the increased metabolism. Above these temperatures, the loss of appetite greatly reduces the maximum rations and maintenance rations soar to cover the rapidly increasing metabolic costs. At these temperatures, the maximum rates are poorly predicted by (27) since the temperatures are near or beyond the scope of $f_3(T)$ to predict RMAX.

If E_n were constant over temperature and size, then (27) would be a simple prediction of GMAX. Preliminary investigations of E_n using the equations developed for RMAINT, RMAX, and GMAX revealed that E_n is probably not constant. There is little information in the literature that documents E_n at maximum rations since maintenance rations must also be known. For the purpose of simulation GMAX is best described by the product of (25) and (26), i.e.,

$$GMAX = \left(a_1 + a_2T + a_3T^2 + a_4T^3 + a_5T^4\right)\left(a_6W^{-a_7}\right) \qquad (28)$$

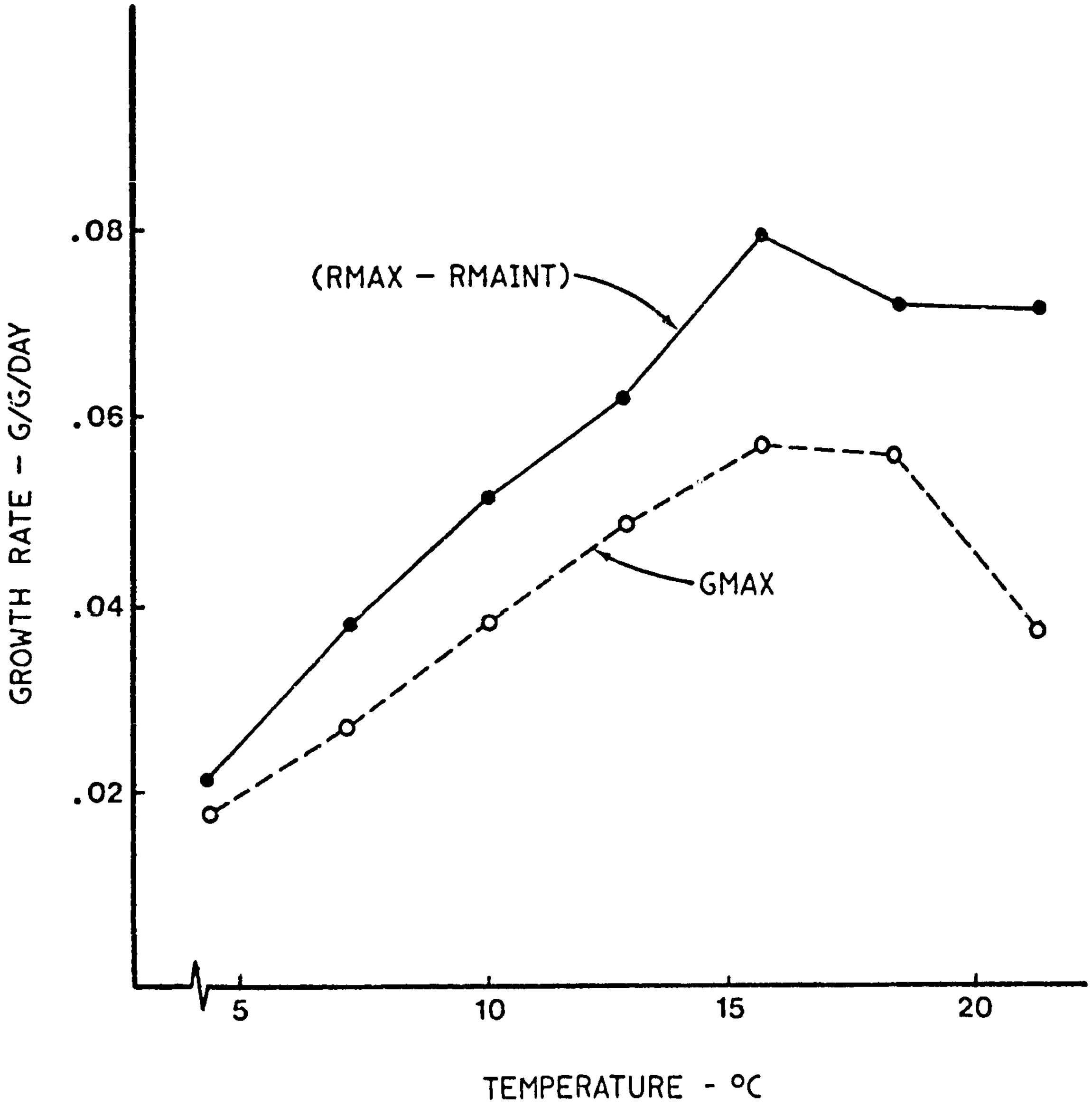


FIGURE 11. The temperature relationships of GMAX and (RMAX - RMAINT) for a 1.0 gram fish.

PRELIMINARY DEMONSTRATION OF THE PROPOSED GROWTH EQUATION

At this stage of development it is desirable to test the growth model's performance in predicting specific growth rates for a wide range of temperatures, fish sizes and daily rations. Most of the published experiments are inadequate or are insufficiently documented to provide the needed test data. Usually one of the three variables is not held constant or is allowed to vary in such a manner as to be confounded with one of the other variables. A unique set of unpublished data from an experiment designed to test the growth response of coho fingerlings fed various rations of the OPR-I were made available by Mr. Dave Leith of the Fish Commission of Oregon State. For the most part, these data were not used in the development of the model.

The experiment was designed as a series of six trials numbered 4 through 9 with eighteen aquariums per trial. Temperatures were held constant at three levels, 4.4, 10.0, and 15.6°C (40, 50, and 60°F) throughout the experiment. This design provided 6 separate lots of fish per temperature per trial. Trials 4 through 7 ran for 2 weeks and trials 8 and 9 ran for 3 weeks. The approximate numbers of fish per aquarium were 64 for trials 4 and 5, 33 for trials 6 and 7, and 14 for trials 8 and 9. The number of mortalities was negligible throughout the experiment. The fish were from the 1962 brood of Columbia River Coho. On the first day the lots of fish in each aquarium were weighed and then fed for the following seven days according to schedule. On the eighth day the lots were reweighed.. The averages of the initial weekly weights were about 2.7 grams per fish for trials 4 and 5, 10.5 grams for trials 6 and 7, and 22.8 grams for trials 8 and 9. The feeding frequencies were 3, 5, or 7 days per week, two meals per feeding day, for the even numbered trials and 2, 4, or 6, two meals per feeding day, for the odd numbered trials. Two aquaria for each of the three temperatures were assigned to one of the three feeding schedules. At these schedules daily rations ranged from near maintenance to almost maximum levels. The moisture content of OPR-I was approximately 32%.

Figures 12 through 20 graphically display the ability of the proposed growth model to predict the specific growth rates observed for this set of data. The observed specific growth rates were calculated on the basis of exponential growth of the lot in each aquarium for the 8 days, i.e.,

$$g_{obs} = \left(\log_e W_{L,1} - \log_e W_{L,0}\right)/8$$

where $W_{L,0}$ is initial weight of lot in grams, and $W_{L,1}$ is weight of the lot 8 days later. The observed daily rations were the weekly total food consumed by the lot divided by initial lot weight divided by 8 days. The predicted specific growth rates, g_{pred}, were calculated by (3) where RMAINT, RMAX, and GMAX were estimated by (11), (12), and (27) respectively. The recommended values for the string of a_i and ℓ_i coefficients were used in

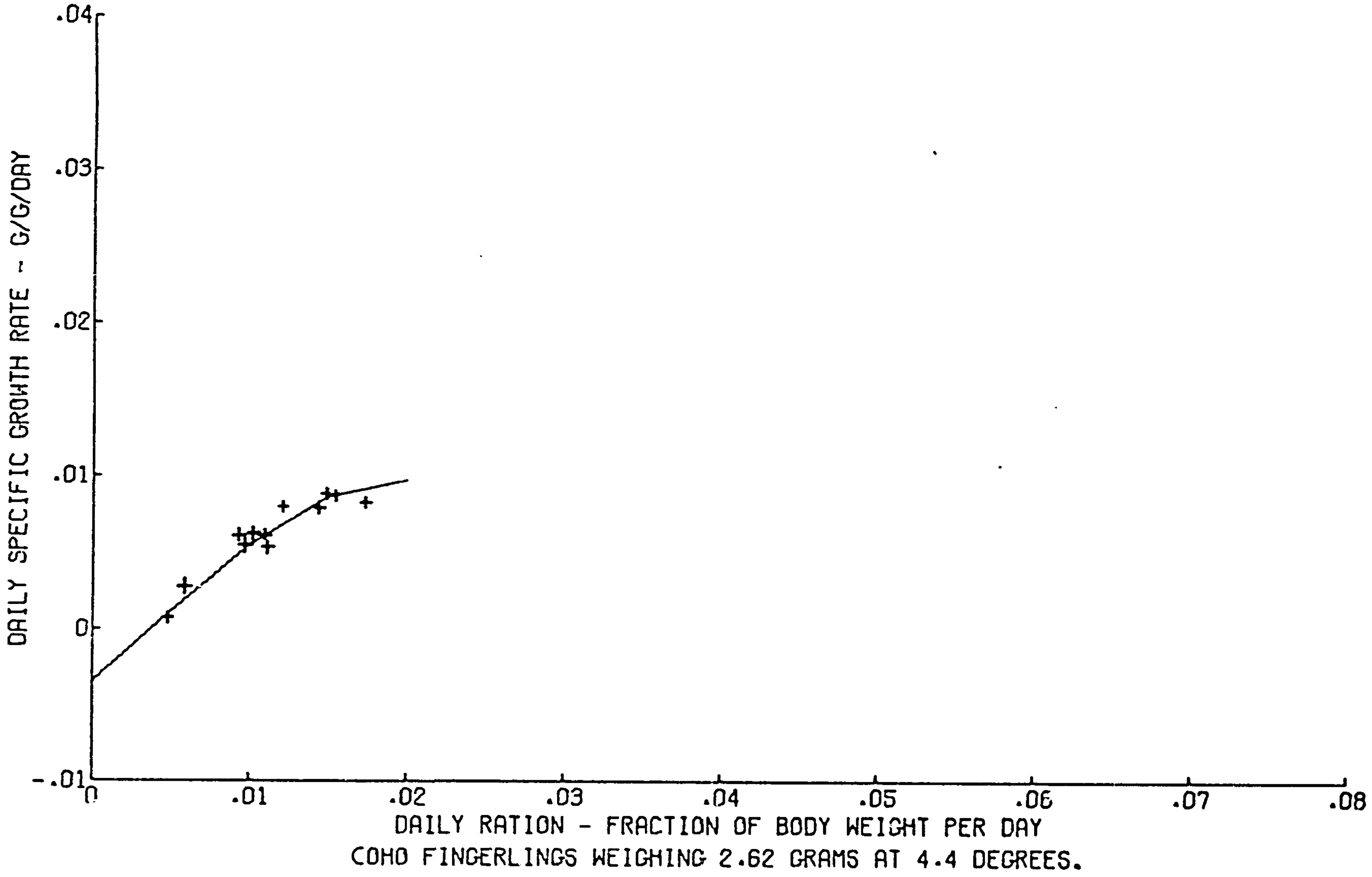


FIGURE 12. The observed (+) and predicted (——) daily specific growth rates for 2.62 gram coho fingerlings held at 4.4°C in the Oregon food-growth experiment.

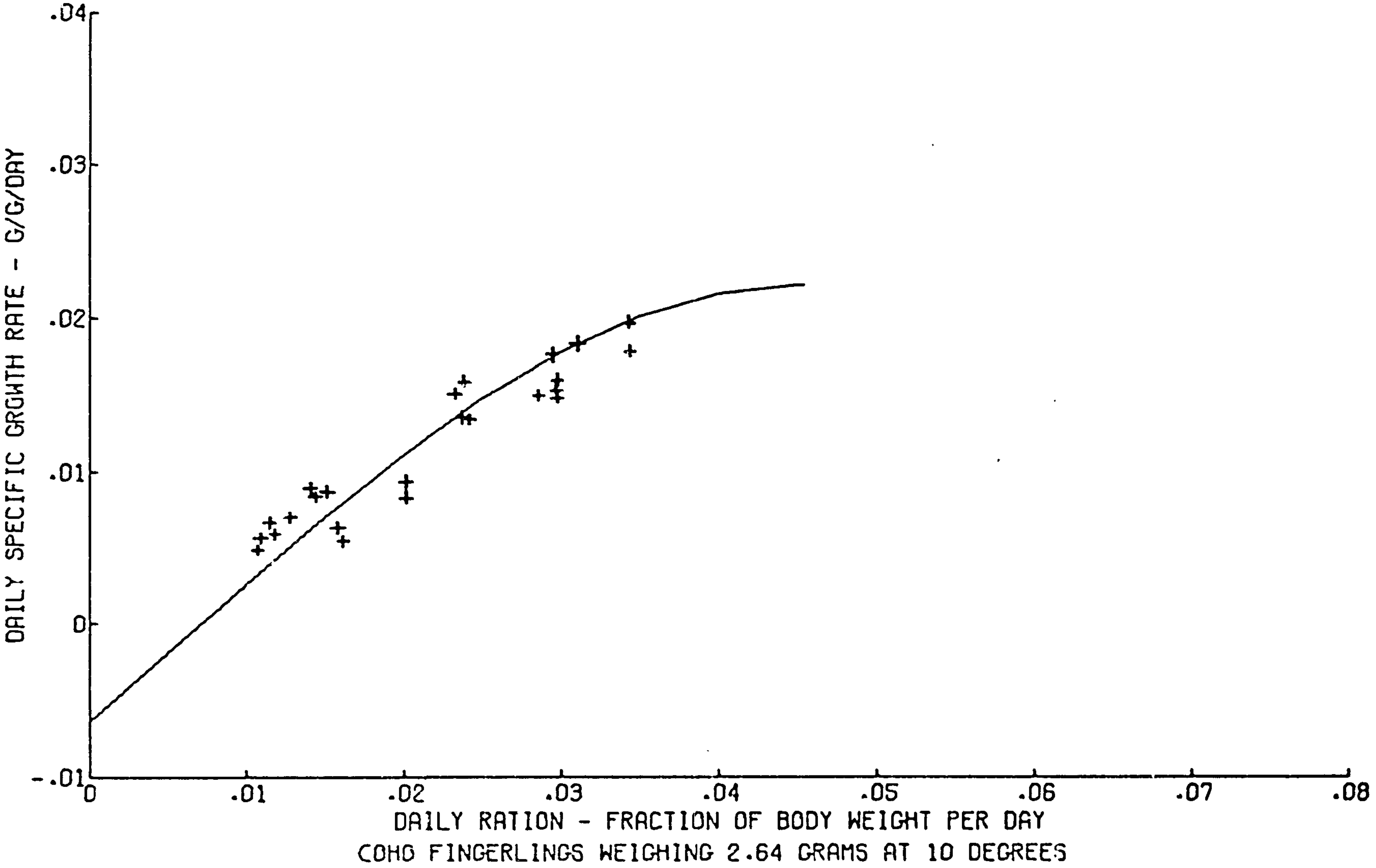


FIGURE 13 The observed (+) and predicted (——) daily specific growth rates for 2.64 gram coho fingerlings held at 10°C in the Oregon food-growth experiment.

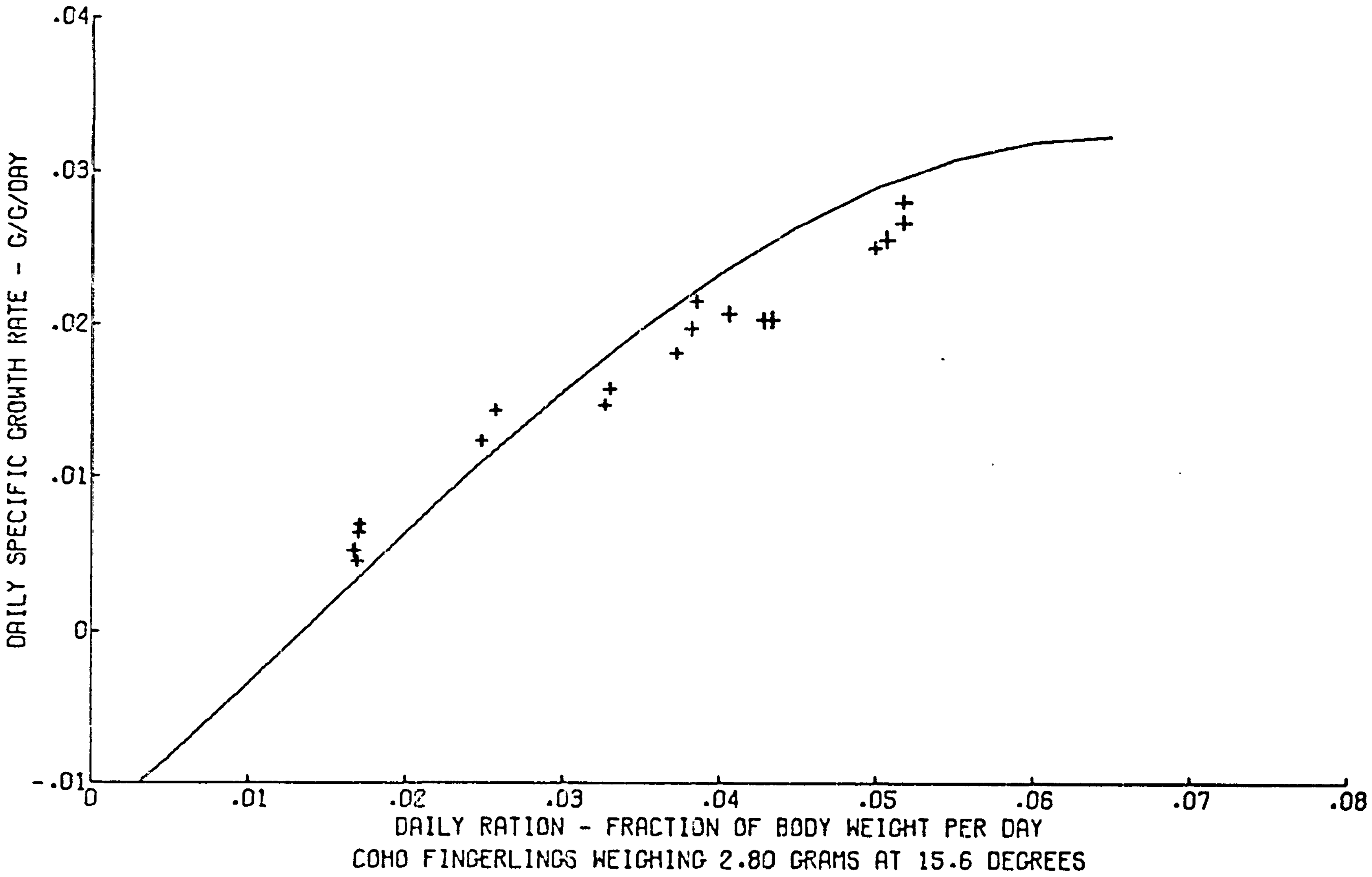


FIGURE 14. The observed (+) and predicted (——) daily specific growth rates for 2.80 gram coho fingerlings held at 15.6°C in the Oregon food-growth experiment.

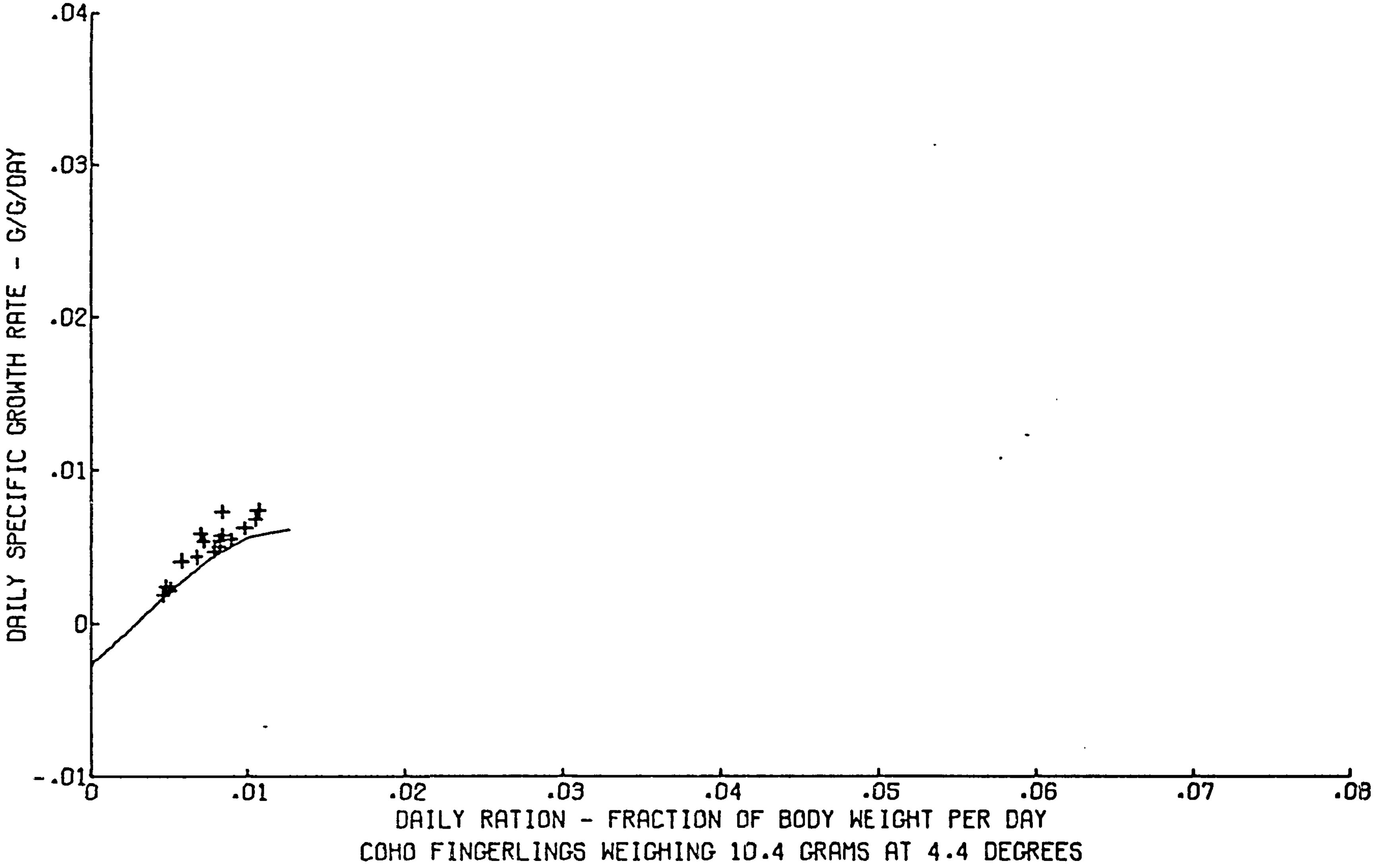


FIGURE 15. The observed (+) and predicted (——) daily specific growth rates for 10.4 gram coho fingerlings held at 4.4°C in the Oregon food-growth experiment.

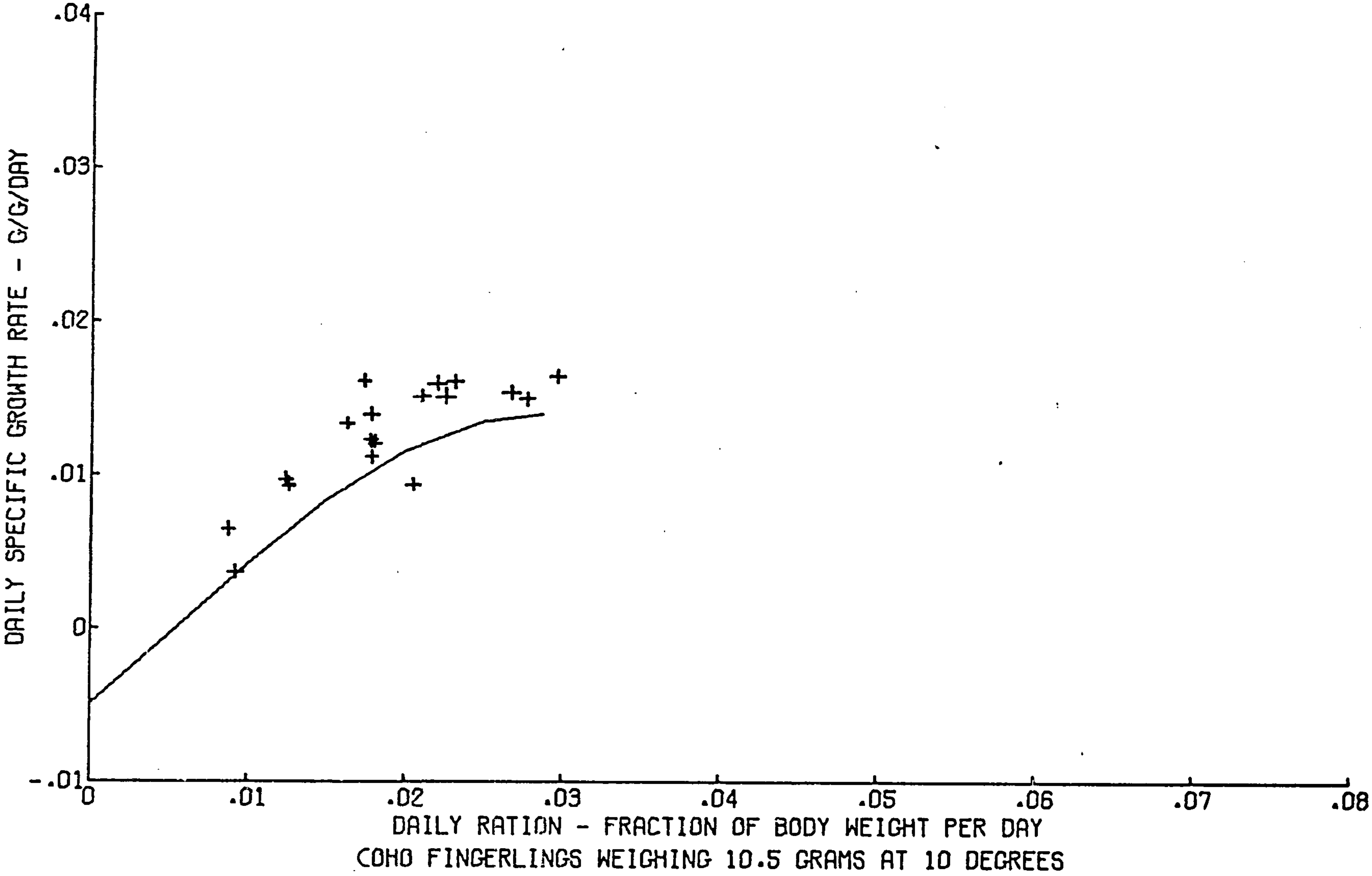


FIGURE 16. The observed (+) and predicted (——) daily specific growth rates for 10.5 gram coho fingerlings held at 10°C in the Oregon food-growth experiment.

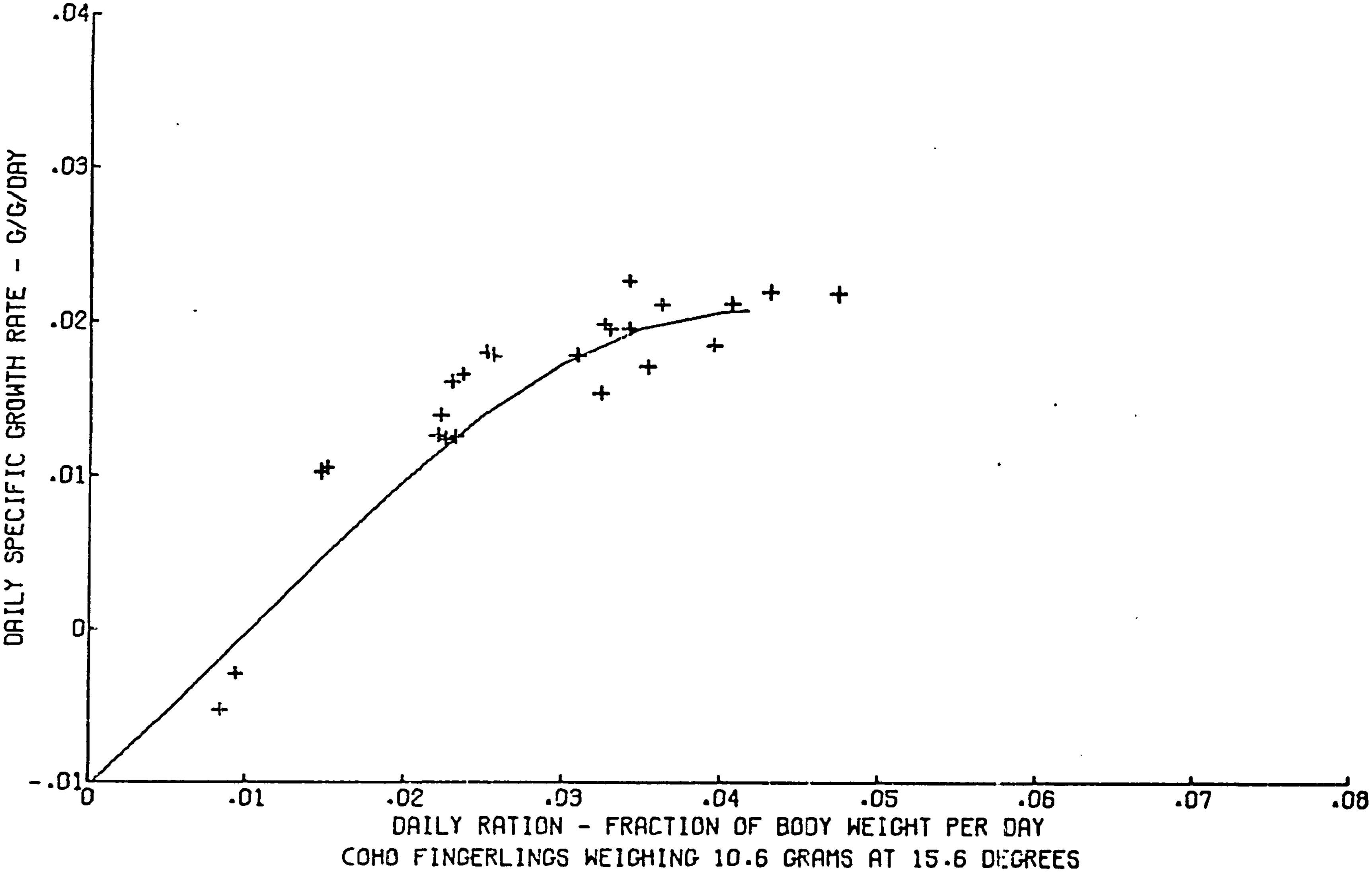


FIGURE 17. The observed (+) and predicted (——) daily specific growth rates for 10.6 gram coho fingerlings held at 15.6°C in the Oregon food-growth experiment.

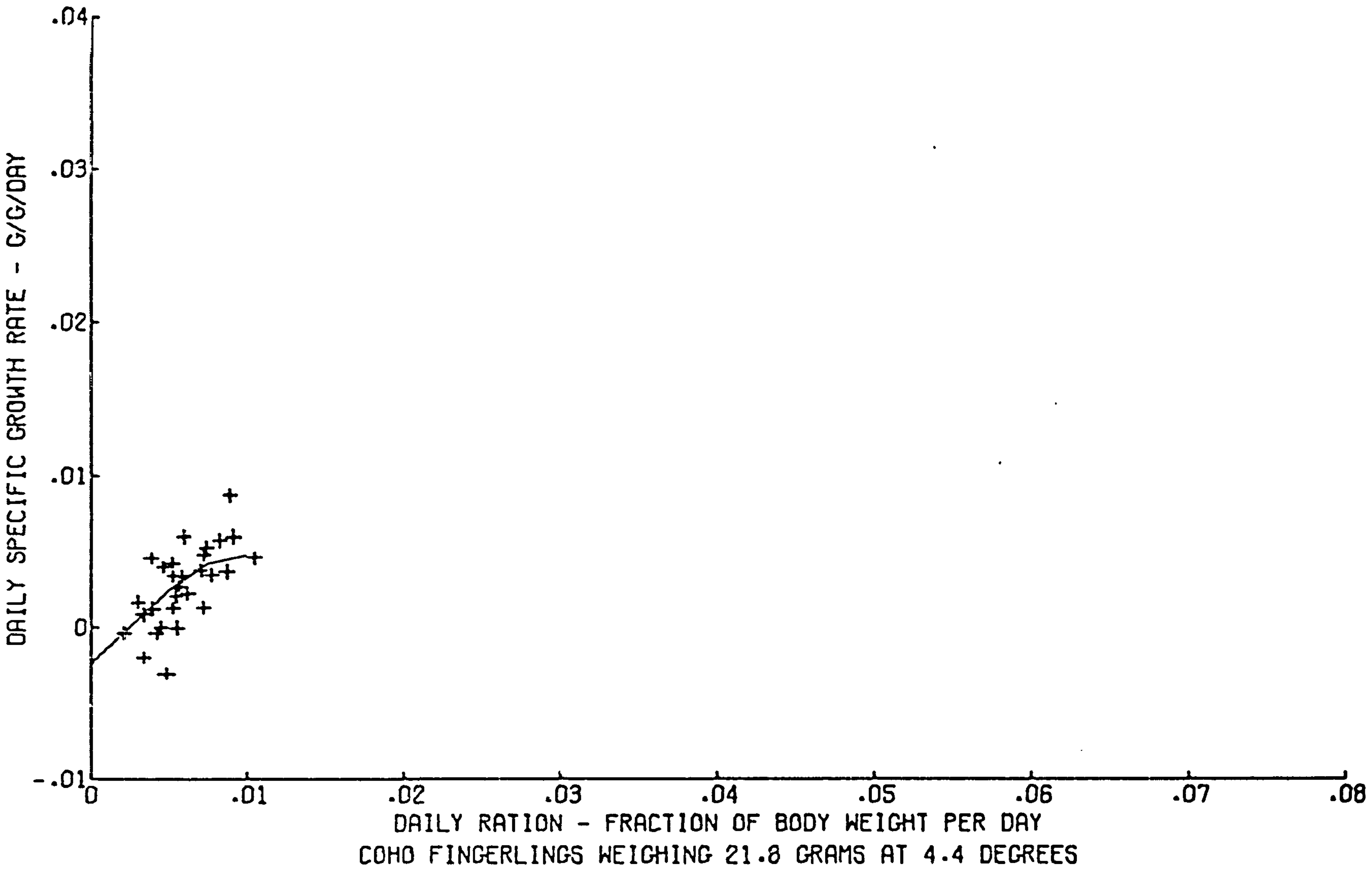


FIGURE 18. The observed (+) and predicted (——) daily specific growth rates for 21.8 gram coho fingerlings held at 4.4°C in the Oregon food-growth experiment.

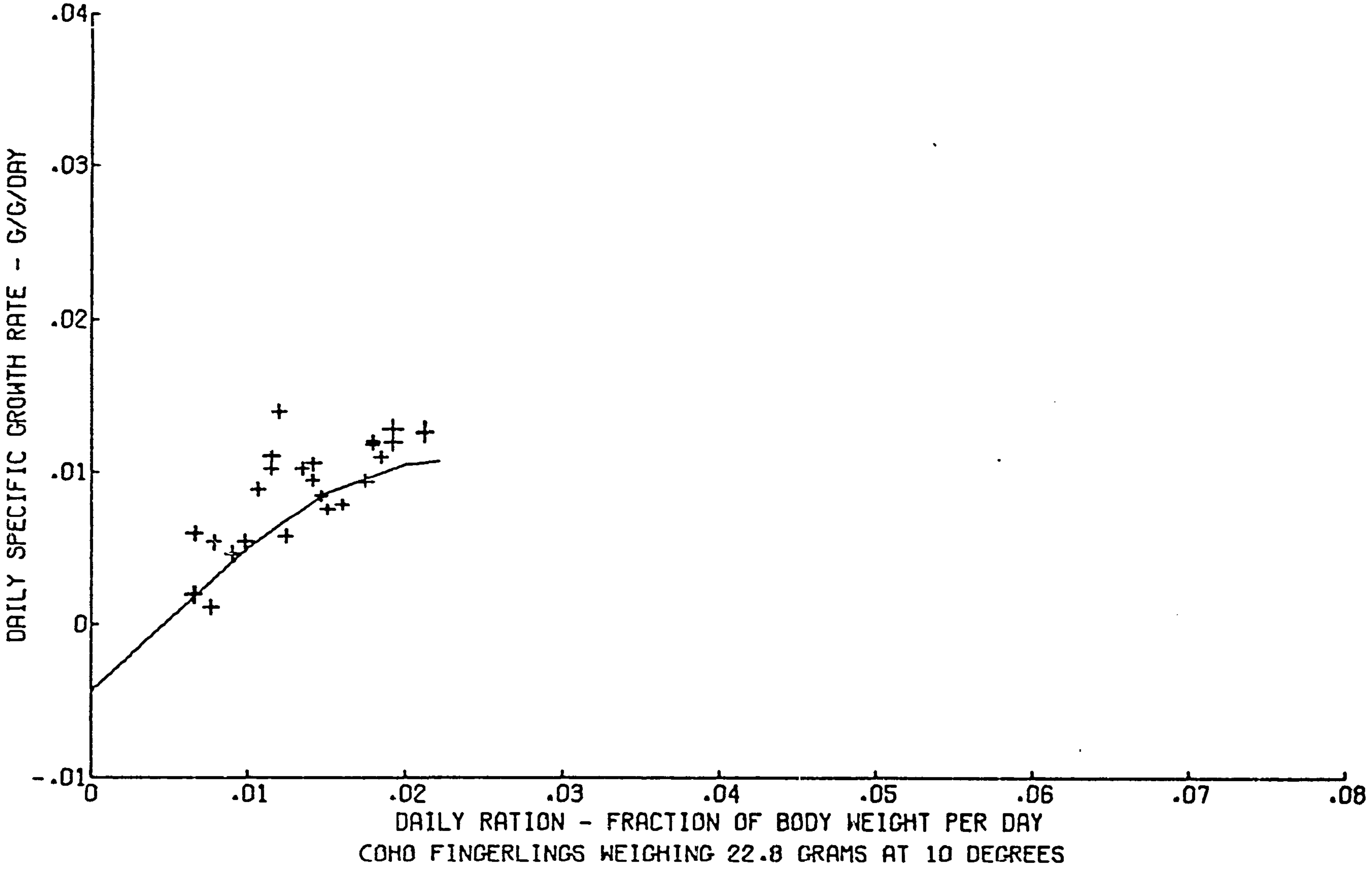


FIGURE 19. The observed (+) and predicted (——) daily specific growth rates for 22.8 gram coho fingerlings held at 10°C in the Oregon food-growth experiment.

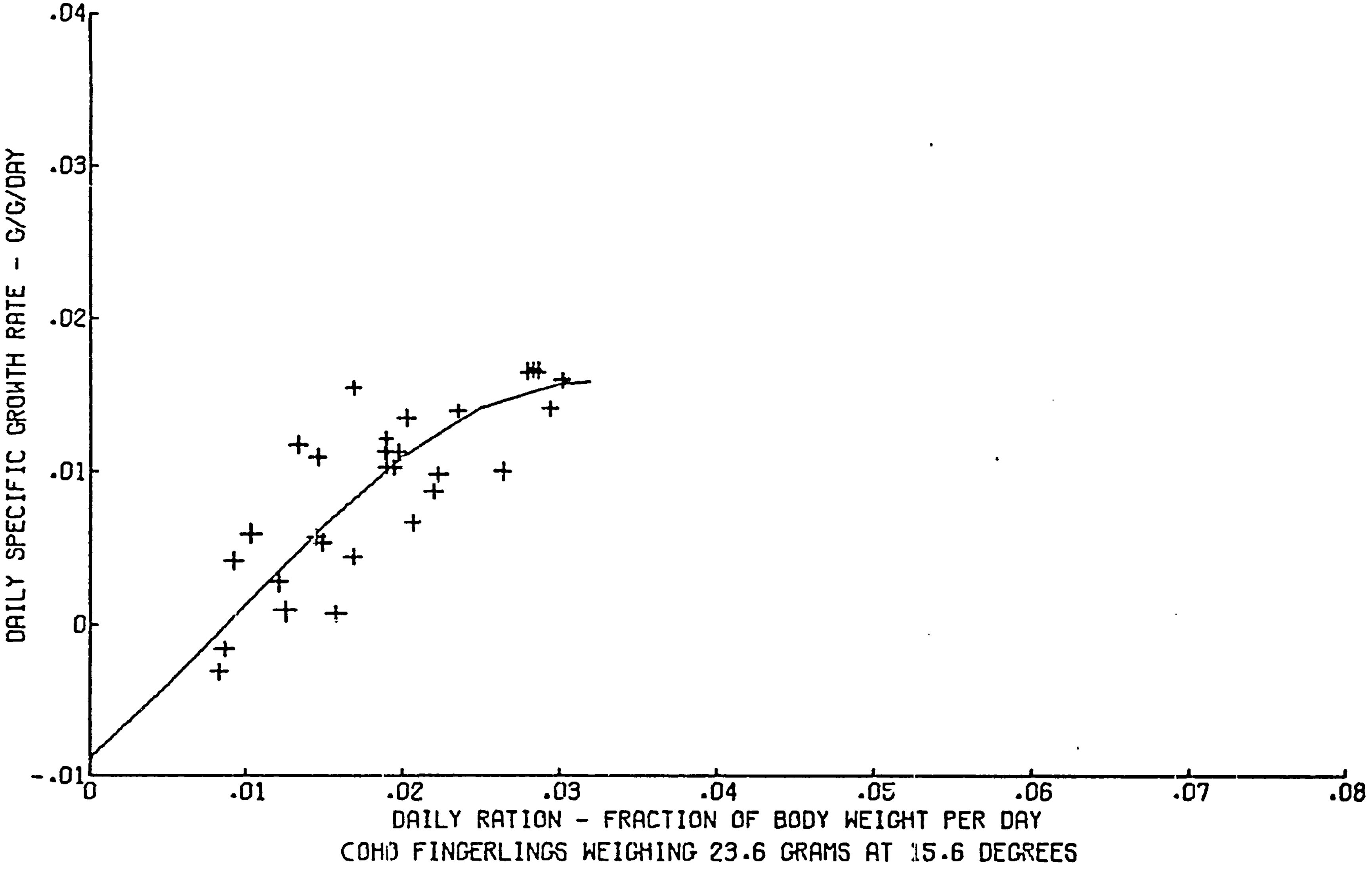


FIGURE 20. The observed (+) and predicted (——) daily specific growth rates for 23.6 gram coho fingerlings held at 15.6°C in the Oregon food-growth experiment.

these calculations. They are

$a_1 = -15.949$
$a_2 = 1.3849$
$a_3 = -0.046018$
$a_4 = 0.00069698$
$a_5 = -0.0000038991$
$a_6 = 0.0304$
$a_7 = 0.3333$

$\ell_1 = 0.0397$
$\ell_2 = 0.0280$
$\ell_3 = 0.0236$
$\ell_4 = 0.2000$
$\ell_5 = 8.82$
$\ell_6 = 2.51$
$\ell_7 = 0.171$
$\ell_8 = 0.3333$

Similar trials were combined to give nine food-growth curves one for each combination of size and temperature. Two sets of predicted values were calculated for each of the nine food-growth relationships. In both cases the observed daily rations and temperatures were used as input, but different weight values were used. In the first case the overall average of initial weights per fish was used to calculate the predicted curves shown in Figures 12 through 20. In the second case the predicted rates were calculated from the weekly observations on each individual lot. For this latter case the differences between the predicted and observed specific growth rates ($g_{pred} - g_{obs}$) were measured and are summarized in the histogram shown in Figure 21. The data from the lots fed 7 days per week were used in the construction of the Oregon maximum ration feeding chart. This includes about one-sixth of the data points. Since the coefficients in the RMAX function were estimated from this

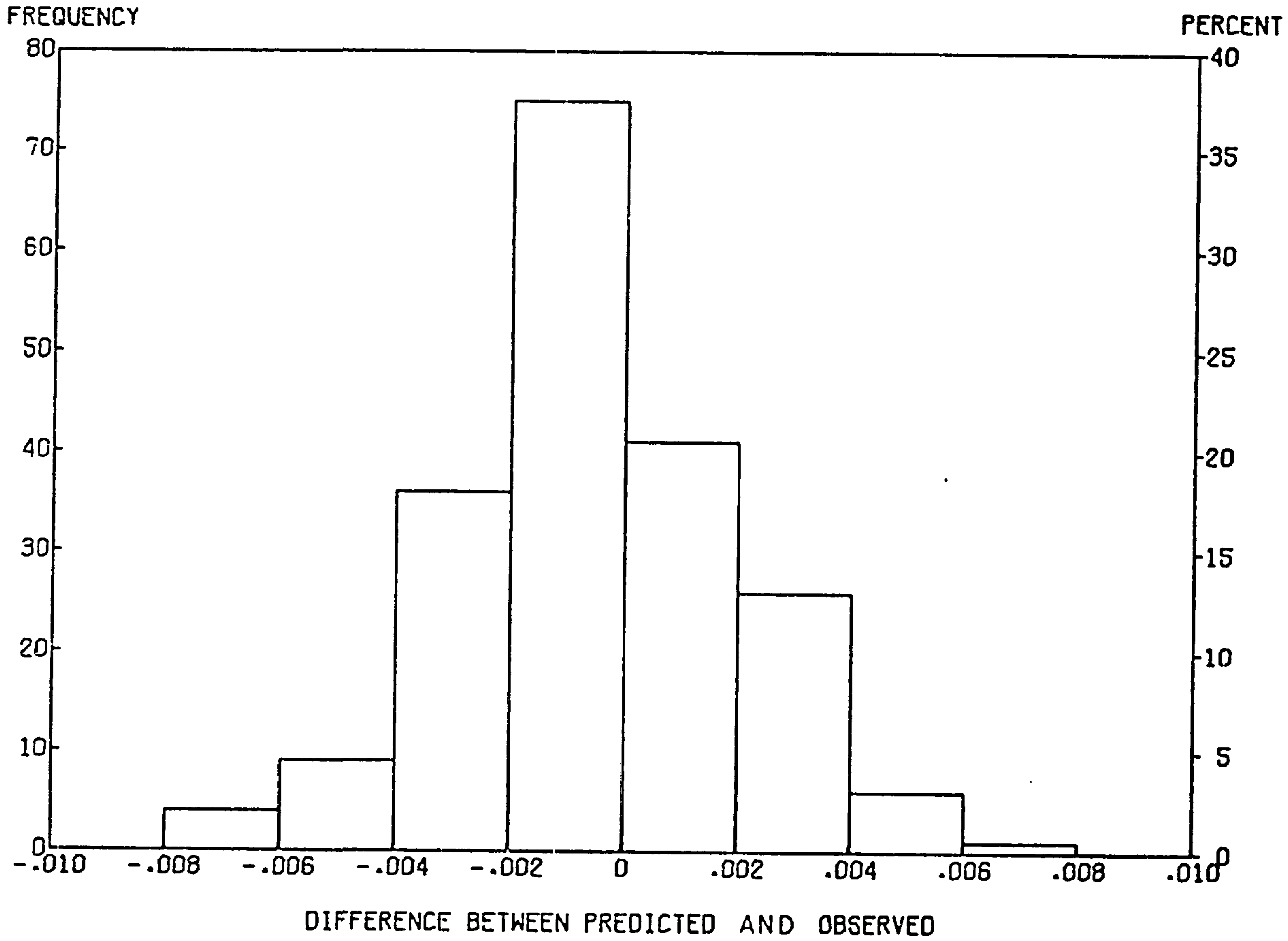


FIGURE 21. The frequency distribution of the predicted minus observed values of the daily specific growth rates for all test lots of coho fingerlings in the Oregon food-growth experiments.

chart originally, the growth equation is not totally independent of these observed values. Some outliers that may have resulted from insufficient acclimation were discarded from the analysis.

Each of the predicted curves shown in Figures 12 through 20 could be criticized as they are probably not the best fit in terms of minimizing the sum of squares error. The Figures are drawn to the same scale for easy comparison between conditions. In general the curves provide good predictions of specific growth rates for the wide range of experimental conditions, especially considering the coefficients are the same in all cases. This is also reflected in the approximately normal curve outlined by the histogram in Figure 21. In this case the mean of the deviation of (g_{pred} - g_{obs}) is -0.0005 and the range is -0.008 ±0.007. This suggests that the growth model with the above coefficients insignificantly underestimates the specific growth rate for these data on the average. These data point out the importance of fish size in determining growth rates. This test of the model demonstrates its ability to predict growth for a wide range of fish sizes, daily rations and temperatures, it does not necessarily verify the correctness of equation forms or coefficient values.

DESCRIPTION OF THE COMPUTER SIMULATION MODEL, GROWTH

Program assemblage

The primary purpose of developing the proposed growth equationsis to predict the growth of salmonids reared in Pacific Northwest hatcheries. The computer program, GROWTH, was assembled to test the effectiveness of the equations in predicting the growth of salmonids reared in these circumstances. The program is written in Fortran IV for the CDC 6400 computer. A users guide (reproduced in Appendix I) and a program listing (number FRS 741) are available on request from the Fisheries Analysis Center, College of Fisheries, University of Washington, Seattle, Washington 98195. The basic schemes in GROWTH for inputting data, indexing time series variables and outputting results were borrowed from the early 1972 version of HATCH, described by Rasch (1972). Essentially GROWTH is an extensively abridged and modified version of HATCH and simulates only the biology of fish growth. The sectors in HATCH describing hatchery water requirements, fish handling costs, fish planting operations, and the sport and commercial fisheries were eliminated. The capacity of HATCH to handle 12 values per variable per year was increased to 104 values per 2 years. Also the capacity of HATCH to handle three lots of fish was reduced to one lot. These modifications allowed the user to follow one lot of fish for two consecutive years. Previously, monthly input data could not vary between years. The data are read into the computer using the free-field format of the KEYWRD subroutine (Gales and Sharpe, 1971 MS). The simulation results are tabulated for each time interval using the standard formats or they may be plotted using the new routine SIMPLOT (Links, 1972). GROWTH was also programmed to allow multiple runs for each job submitted to the computer. The flow of the GROWTH program is briefly diagrammed in Figure 22.

Keeping track of time within GROWTH is confusing but it is essential for accurate simulation and data input and output. There are two clocks in GROWTH that indicate time. The "counter" tells the time by counting the iterations of time intervals during simulation. The "calendar" measures time in monthly units, 28 or 30.4 days long depending on user specification. The "calendar" is the buffer between the "counter" and the user with his hatchery or laboratory data of periodic fish weights and weekly or semimonthly averages of water temperature and daily rations. The user specifies the dates of the data input in "calendar" months. During simulation these are converted to "counter" dates for calculating the growth rates and then converted back to "calendar" dates for outputting purposes. The reasons for the two systems are to add realism to the model and to provide flexibility in the length of the time interval between growth calculations and data print out. Growth can be incremented either weekly or semimonthly. The results can be printed out either weekly, semimonthly, or monthly. If the results are printed out semimonthly or monthly, then the values of the daily ration and temperature used in the growth calculations are the average of the two or four weekly input values.

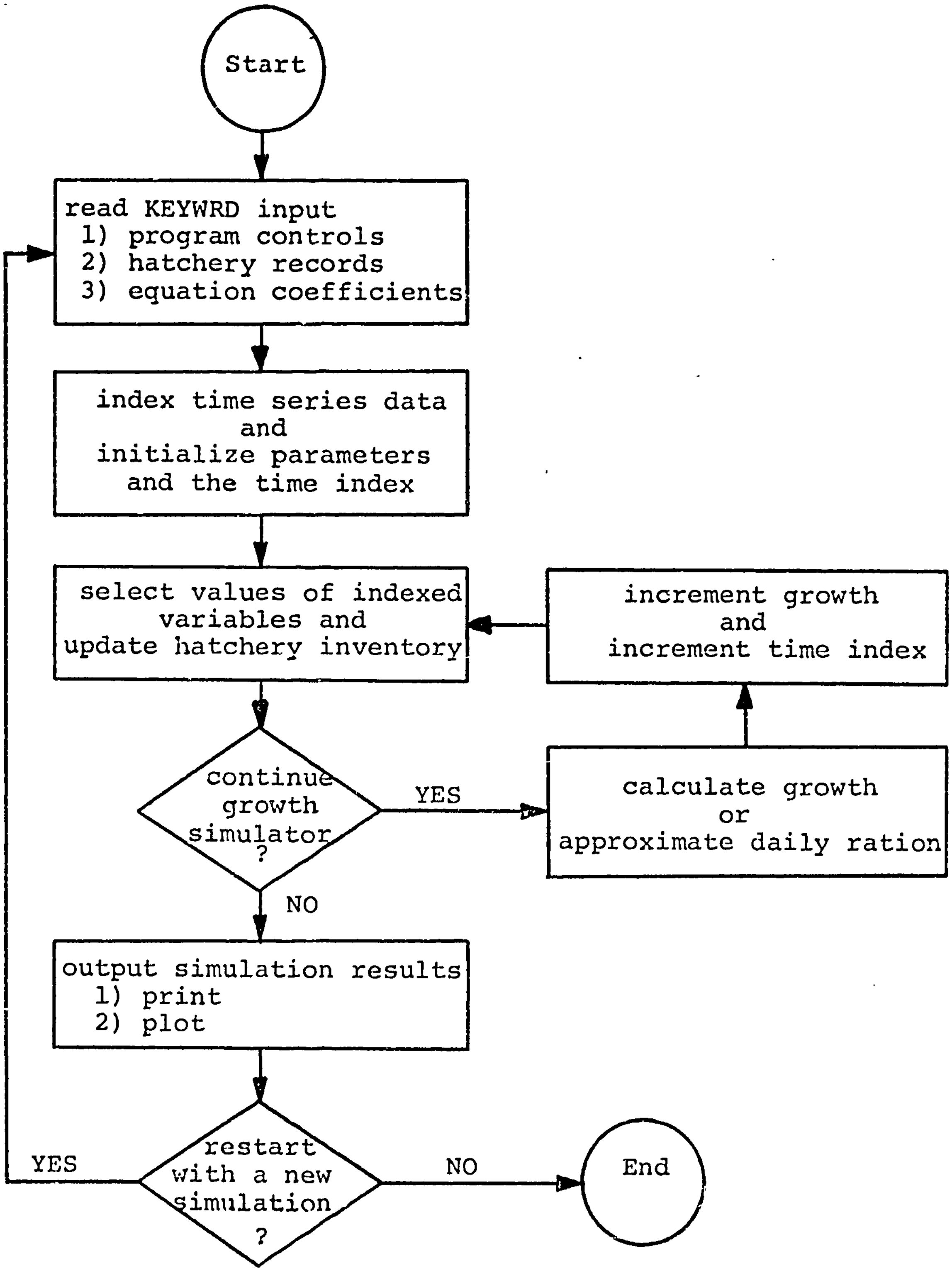


FIGURE 22. A brief flow diagram of the computer simulation model GROWTH.

The lengths of the time intervals are 7 or 7.6 days for the weekly interval, 14 or 15.2 days for the semimonthly interval, and 28 or 30.4 days for the monthly interval. The alternative numbers of days for each interval allow the user to simulate growth on the basis of 7 days in a week and 13 months in a year or 7.6 days in a week and 12 months in a year. The "calendar" date, 1.0, and the "counter" time, 1, refer to January 1 of the first year. December 1 of the first year in "calendar" time is 12.0 for 30.4 days per month or approximately 13.0 for 28 days per month. December 1 has a variety of "counter" equivalents depending on the length of the basic time interval.

Special features

The versatility of GROWTH is increased by three special features not yet described. The first of these adjusts rations for the moisture content of the diet and fish flesh. The second is an algorithm that predicts the daily ration necessary to grow fish at some predetermined rate. The third provides a means of quantitatively measuring the deviation between the predicted and observed rations for the entire simulation.

The coefficients of the proposed growth model were based on dry weight measurements of daily ration and fish weight. On the other hand, hatchery records are based on wet weight measurements. Modern hatchery diets vary between a dry or a moist food. The dry diets like the Abernathy dry pellet and the various trout diets vary between 6 and 10% moisture (J. E. Banks, personal communication; Dr. D. L. Horak, personal communication). When dry diets are stored, their moisture content may increase to as high as 10%. The moist diets like OPR vary between 27 and 37% moisture depending on the ingredients (Crawford and Law, 1972; Fowler and Banks, 1970). The Oregon formulation OPR-1 composed of 40% wet fish is about 33% moisture and OPR-2 which is 30% wet fish is almost 30% moisture (Crawford and Law, 1972). The moisture content of the diets is taken into account in GROWTH by multiplying the hatchery daily ration data by a correction factor that converts the values to a dry weight basis, i.e.,

$$R_{dry} = \left((1-FDMCT)/(1-FHMCT)\right) R_{wet}$$

where FDMCT is the moisture content of the diet and, FHMCT is the moisture content of fish flesh. The moisture content of whole fish has been measured for numerous salmonids. A value of 75% is generally applicable. Phillips (1969) noted that hatchery trout contain between 75 and 80% water. Brett, et.al. (1969) measured the moisture content of sockeye fingerlings reared at various feeding levels. For starved fish they observed fish with a water content of more than 80%. At the other extreme fish fed excess rations had a content near 71%. Brett and Sutherland (1970) confirmed that sockeye fingerlings fed maximum rations may be around 70% water. In general the moisture content of fish depends on their feeding history (Brett, et.al., 1969).

Specific growth rates calculated from wet weights do not necessarily equal the values based on dry weights if the moisture content of the flesh is fluctuating. Wet weight measurements of growth will underestimate the actual increase in dry cellular tissue if the moisture content is decreasing. The opposite is also true, i.e., rates of growth derived from wet weights will overestimate the dry weight change if the moisture content is increasing. For the purpose of this dissertation the moisture content of fish flesh is assumed to be a constant 75%.

The second feature is an alternative procedure that determines the daily ration necessary to grow fish to a predetermined size by some future date for a given temperature schedule. Two alternative schemes exist. First, the necessary daily ration can be estimated from the closed form expression for R derived from (3), i.e.,

$$R = \mathrm{RMAINT} + 2/\pi(\mathrm{RMAX} - \mathrm{RMAINT}) \arcsin(g/\mathrm{GMAX})$$

The value of g can be estimated by (2) using the predetermined weights. If the duration of the printout interval is equal to the duration of the growth interval, then this expression will find a precise solution for R. On the other hand, if there is more than one growth interval, then the values of RMAINT, RMAX, and GMAX used in the equation, must be the average of those for each growth interval. This also requires interpolating intermediate values of the desired weight. All this results in some variation that can prevent a precise solution for R.

An alternative method for estimating daily ration is an iterative procedure that continually adjusts daily rations by a determined amount until the corresponding growth calculated from the proposed equations nearly equals some specified value. The difficulty is finding a criterion with which to adjust the rations so that calculated growth converges on the desired size in just a few iterations. A quantitative examination of the relation between growth and daily ration using the growth equations revealed a possible criterion. It was found that for intermediate daily rations a ± .01 g/g/day change resulted in approximately a 2% change in the possible size at the end of one week for a number of initial sizes and a variety of temperatures. In terms of the marginal food conversion efficiency, MFCE, as defined earlier this is

$$dW_{t+1}/dF \approx \frac{(W_1 - W_2)/W_t}{t(R_1 - R_2)} \sim \frac{.02}{.01 \times 7} \sim .30$$

If the notation is altered to

$$dW_{t+1}/dF \approx \frac{(W_D - W_i)/W_i}{(R_{i+1} - R_i)t} = \text{MFCE}$$

where W_D is the desired size at time t+1

W_i is the size calculated for time t + 1 using the ration for the i^{th} iteration

R_i is the value of the ration in the i^{th} iteration

R_{i+1} is the value of the ration in the $i+1^{th}$ iteration

t is the length of the time interval in days then a solution for R_{i+1} is

$$R_{i+1} = \frac{(W_D - W_i)/W_i}{t(MFCE)} + R_i \qquad (29)$$

In this way the value of the ration can be systematically adjusted by incrementing i and solving for R_{i+1} until the condition

$$|W_D - W_i)/W_i| \leq \text{ specified minimum value } \sim .01$$

is satisfied. The number of iterations necessary to meet this inequality is generally minimized when the value of MFCE is near its maximum.

The first procedure described consumes less computer time and can provide an adequate solution for R, depending on user requirements. The second procedure is more time consuming but it can find the R that will grow fish to the exact desired weight. For the purpose of this dissertation the latter procedure is used.

The third feature is a criterion for measuring the quality of a simulation. With the large number of coefficients and the various combinations of species, diets, rearing facilities, etc. that can occur, it is unlikely that the original coefficients will reproduce the growth pattern in all circumstances. When it is necessary to adjust coefficients to improve the predictions, it becomes necessary to establish criteria which will measure the improvement. The criterion then provides the basic information from which to choose the values of the coefficients that best simulate the observed growth pattern. Generally in statistics the criterion is some form of the sum of squares of the deviations between the observed and predicted values. The term employed here is the root mean square, RMS, which is

$$\mathrm{RMS} = \left(\left(\sum_{t=1}^{n} \left(Y_{obs,t} - Y_{pred,t}\right)^{2}\right) \Big/ n\right)^{1/2}$$

where $Y_{obs,t}$ is the observed value of the Y variable at time t

$Y_{pred,t}$ is the predicted value of the Y variable at time t

n is the number of time intervals or observations.

With the development of (29), either the deviation between the observed and predicted fish weights or daily rations can be used. The deviations for fish weights have inherent problems resulting from serial correlation in weight. The estimated growth depends to some extent on the size of the fish. If an error is made in one time interval, subsequent growth will also be in error. The effect of this type of error can be minimized and contained by estimating the ration that grows fish at the rate equal to the observed using (29). For this reason it is recommended that the RMS criterion measure the deviations between the observed and predicted daily rations, i.e.,

$$\mathrm{RMS} = \left(\left(\sum_{t=1}^{n} \left(R_{obs,t} - R_{pred,t}\right)^{2}\right) \Big/ n\right)^{1/2} \qquad (30)$$

Unfortunately there is no probability theory associated with this criterion since the distribution of $R_{pred,t}$ is unknown.

SIMULATION OF THE GROWTH OF ACTUAL HATCHERY REARED SALMONIDS

Preliminary results

To test the effectiveness of the proposed growth model in predicting the growth of hatchery reared salmonids, the records on recent broods of fall chinook, spring chinook and coho salmon were retrieved from seven Pacific Northwest hatcheries listed in Table 3. Of the nearly 100 separate lots of fish that could be identified in these records, about 30 were selected for test purposes. Test lots were selected on the basis that

(1) the records on weekly temperatures and total weekly food consumption were continuous for more than 2 months,

(2) the records included periodic estimates of the average fish weight,

(3) the numbers of fish on hand, transferred or planted were well documented,

(4) the lot did not suffer heavy mortalities from disease,

(5) weekly food conversion factors were generally greater than 1.0, and

(6) the lot would provide an interesting test of the growth equations in that it was not repetitious of other selected lots.

The input data for GROWTH, including weekly values of

TABLE 3. The list of hatchery records from which test lots were selected.

HATCHERY	SPECIES	BROOD YEAR
Washington Department of Fisheries		
Green River	Fall Chinook	1969 and 1970
Klickitat	Fall Chinook	1968 and 1969
	Spring Chinook	1968 and 1969
	Coho	1968 and 1969
Minter Creek	Fall Chinook	1968 and 1969
	Coho	1968 and 1969
Fish Commission of Oregon		
Big Creek	Coho	1968 - 2 experimental lots
Bonneville	Coho	1969 and 1970
Cascade	Coho	1969 and 1970
Sandy	Coho	1970

fish weight, daily ration, and water temperature, were tabulated for each test lot. The fish in hatchery lots are normally sampled semimonthly or monthly to estimate their average weight. Estimates of the average weight at the start of each week are required though for the simulation. These values were linearly interpolated from the monthly records. The average daily ration for each week was calculated from the weekly total of food consumed by the lot divided by the product of the fish size at the start of the week times 7 days. The average size of the fish at the start of the week was used rather than the average size for the entire week because in the process of simulating growth, the future size of the fish is unknown at the start of the week. Also food consumption was divided by the number of fish at the start of the week rather than average number of fish surviving during the week. The error is insignificant if the weekly loss is small relative to the total number in the lot. Normally only the daily maximum and minimum water temperature are documented in hatchery records. Consequently, the average of the 14 daily maximum and minimum values was taken as weekly average water temperature. The potential for errors in hatchery data is large. The source of these errors and their influence on the simulation are discussed in a later section.

In all cases the simulation operated on the basis of 7 days per week and 28 days per month. The mortality of the fish was set at zero for the simulations although this was not true in the real world. Weekly averages of daily ration and water temperature were read in but the values were automatically averaged for each semimonthly period. Specific growth rates were calculated weekly and average weights incremented weekly but for purposes of brevity only the semimonthly weights and the semimonthly average of specific growth rates were printed out

For many of the test lots, preliminary simulations of the fish growth, using the previously recommended values of the coefficients, indicated that the predicted growth rates were less than the observed values for wide ranges of temperature and size. The exceptions were during periods when the fish were fed rations near the maintenance level. In these cases, the predicted growths were consistently greater than zero. Similar discrepancies occurred in the simulations of test lots selected from the Klickitat hatchery where water temperatures are approximately 10°C (50°F) year around. This suggests that the functions of temperature $f_1(T)$, $f_3(T)$, and $f_5(T)$ might not be at fault. Furthermore the value of the observed daily ration exceeded the estimate of the maximum daily ration in only a few instances, indicating that the coefficients for the RMAX expression are approximately correct. Of the four remaining coefficients, ℓ_1 and a_6, the maintenance ration and maximum specific growth rate of a 1.0 gram fish at 10°C (50°F) respectively, were judged to need adjusting. The value of ℓ_4 may also need adjusting since in the development of the RMAINT expression, its value varied between .2 and .333. On the other hand, the value of a_7 is probably adequate since it is based on the assumption of isometric growth. Consequently, the coefficients that were the most probable cause of the discrepancies are reduced to ℓ_3, ℓ_4 and a_6.

Readjustment of growth coefficients

There are two alternative strategies for adjusting the values of these coefficients in an attempt to improve the simulation of these sets of data. The first is to conduct laboratory experiments to estimate their values for the conditions of these data. The second strategy is to run the simulation for a set of data a number of times, altering the values systematically each time until the predicted growth sufficiently duplicates the observed or until the RMS attains some minimum value. This latter criterion coupled with the optimization theory from calculus provides an efficient method for determining the values of the coefficients in question that minimize the discrepancies. The RMS surface generated by the numerous simulations for which the coefficient values were systematically altered for each run can be fit by an equation of the form

$$\begin{aligned} \mathrm{RMS} = {} & b_0 + b_1\ell_3 + b_2\ell_4 + b_3a_6 + b_4\ell_3^2 + b_5\ell_4^2 + \\ & b_6a_6^2 + b_7\ell_3\ell_4 + b_8\ell_3a_6 + b_9\ell_4a_6 \end{aligned} \tag{31}$$

where the variables ℓ_3, ℓ_4 and a_6 are the growth parameters varied in the simulations. The coefficients $b_0, b_1, \ldots, b_9$ are estimated by the multiple regression fitting routine. It follows from the theory that the values of ℓ_3, ℓ_4 and a_6 that minimize the RMS are the solution to the three first order partial derivatives of (31) with respect to ℓ_3, ℓ_4 and a_6 set equal to zero, i.e.,

$$\partial RMS/\partial \ell_3 = b_1 + 2b_4\ell_3 + b_7\ell_4 + b_8a_6 = 0$$

$$\partial RMS/\partial \ell_4 = b_2 + 2b_5\ell_4 + b_7\ell_3 + b_9a_6 = 0$$

$$\partial RMS/\partial a_6 = b_3 + 2b_6a_6 + b_8\ell_3 + b_9\ell_4 = 0$$

These can be rewritten in terms of matrix algebra as

$$Bx = b$$

where the matrix $B = \begin{bmatrix} 2b_4 & b_7 & b_8 \\ b_7 & 2b_5 & b_9 \\ b_8 & b_9 & 2b_6 \end{bmatrix}$

the vectors $x = \begin{bmatrix} \ell_3 \\ \ell_4 \\ a_6 \end{bmatrix}$ and $b = \begin{bmatrix} -b_1 \\ -b_2 \\ -b_3 \end{bmatrix}$

From this the solution of x, the values of ℓ_3, ℓ_4 and a_6 that minimize RMS, can be expressed as

$$x = B^{-1}b \qquad (32)$$

In order to find values of ℓ_3, ℓ_4 and a_6 that minimized the general discrepancies in the preliminary simulations, this optimization method was performed on two independent sets of test lots. Table 4 lists the lots in each set. These two sets only include coho lots. If the resulting values of the coefficients would not correct the discrepancies in the chinook simulations, then the plan was to duplicate

TABLE 4. The list of the test lots used in finding the values of ℓ_3, ℓ_4, and a_6 that minimized simulation discrepancies.

HATCHERY	SPECIES	BROOD YEAR	LOT
<u>First Set</u>			
Big Creek	Coho	1964	High ration group
Cascade	Coho	1970	1
Klickitat	Coho	1968	Small grade
Minter Creek	Coho	1968	White River
<u>Second Set</u>			
Big Creek	Coho	1964	Low ration group
Bonneville	Coho	1969	2
Klickitat	Coho	1968	Large grade
Minter Creek	Coho	1968	OPR diet trial group

the process for chinook lots. The combinations of coefficient values for estimating RMS were formed from the apprximate minimum, median, and maximum values of each coefficient. The two sets of the estimated RMS values were fitted to (31) separately with the stepwise regression program, BMD02R (Dixon, 1965). The multiple R^2 was 0.97 and 0.91 for the first and second sets respectively. The elements of B and b, produced by these regression analyses, are listed in Table 5. The solutions of (32) for these B and b were calculated with the computer program EMATRIX (Gales, 1971). The respective estimates of x are $\begin{bmatrix} 0.0365 \\ 0.1958 \\ 0.0383 \end{bmatrix}$ and $\begin{bmatrix} 0.0277 \\ 0.2372 \\ 0.0383 \end{bmatrix}$. The average of these two vectors yields the estimates $\ell_3 = 0.0321$, $\ell_4 = 0.2165$, and $a_6 = 0.0383$. The values of a_6 are surprisingly stable and considerably greater than the previous starting value 0.0304. This higher value should increase the predicted growth rates and thereby reduce the simulation discrepancies. The estimate of ℓ_4 is closer to the original value of 0.2 than to 0.333 which agrees with the conclusions of Paloheimo and Dickie (1966a) and Winberg (1956). Both estimates of ℓ_3 are greater than the previous starting value although the estimates are relatively far apart. The increase in ℓ_3 will increase the estimates of RMAINT in the simulations and thereby reduce the predicted growth rates during maintenance periods.

TABLE 5. The elements of the matrix B and the vector b for the two sets of test data.

MATRIX B	Vector b
First Set	
$\begin{bmatrix} .6344 & -.02126 & -.8666 \\ -.02126 & .002830 & .02802 \\ -.8666 & .02802 & 4.3933 \end{bmatrix}$	$\begin{bmatrix} -.01418 \\ .0008507 \\ .1420 \end{bmatrix}$
Second Set	
$\begin{bmatrix} 1.0983 & -.05801 & -.2467 \\ -.05801 & .005248 & -.01724 \\ -.2467 & -.01724 & 6.2075 \end{bmatrix}$	$\begin{bmatrix} .007194 \\ -.001022 \\ .2270 \end{bmatrix}$

Results for fall chinook salmon

Klickitat hatchery

The Klickitat hatchery on the Columbia River system has records on a number of fish lots that provide interesting tests for the proposed growth model. These are interesting for two reasons; first, the temperature of the hatchery water is relatively stable and usually varies between 8.9 and 11.2°C (48 and 52°F) and second, often the fish are graded into uniform size groups with a different feeding schedule assigned to each group.

The fall chinook salmon from the 1968 brood, Spring Creek stock were selected from a number of identifible lots in the 1968 and 1969 broods. The fish in this lot, totaling 1.8 million, were placed in the hatchery rearing ponds on 26 December 1968. The fish were fed an OPR diet except during the initial feeding period. In early March after one third of the lot was transferred to another hatchery, 1.1 million fry were evenly split into 5 ponds. It is not known if these fish were graded, although at the time of the split the fish averaged 1.34 grams in ponds 21 and 22, 1.09 grams in pond 23, and 1.40 grams in pond 24 and 25.

The growth of the fish in ponds 21, 23, 24, and 25 was simulated beginning on 8 March 1969 (or computer calendar month 3.5) and terminating on 3 May 1969 (month 5.5) 9 days prior to their release. Also the growth for the entire lot with all ponds combined was simulated beginning two weeks earlier when the fish averaged 0.987 grams. Figures 23, 24, 25, and 26 show the success of these simulations. Table 1 of Appendix II lists the weekly input data and the predicted semimonthly specific growth rates and fish weights. The growth predicted for ponds 21 and especially 23 reproduce the observed pattern quite well. The predicted growth for ponds 24 and 25, though, is greater than the observed. A partial explanation of the large discrepancy between the predicted and observed weights for pond 25 could be that the weights recorded for pond 25 may have been estimated from samples of fish from pond 24 because the average weights for both ponds were recorded as identical. Comparisons of ponds 24 and 25 and ponds 21 and 25 indicate the influence of daily ration in controlling the predicted growth rates. In both cases the daily rations for pond 25 were greatest and in both cases the predicted growth rates were greatest. The simulated growth for the entire lot approximates the average observed growth until month 5.0 at which time the predicted weights exceed the observed. This is probably caused by the higher rations fed in ponds 24 and 25. Simulations of the entire lot, started on earlier dates when the fish were smaller, failed in that the predicted growth rates for the earlier weeks were too low. A possible explanation of this is that in the early weeks of rearing, the salmon fry are still receiving some nourishment from their yolk supply. In addition, fry are fed low rations to minimize the wastage of food until the fry learn to feed.

These simulations are important for three reasons. First, the amplitude of the daily and seasonal cycles of the

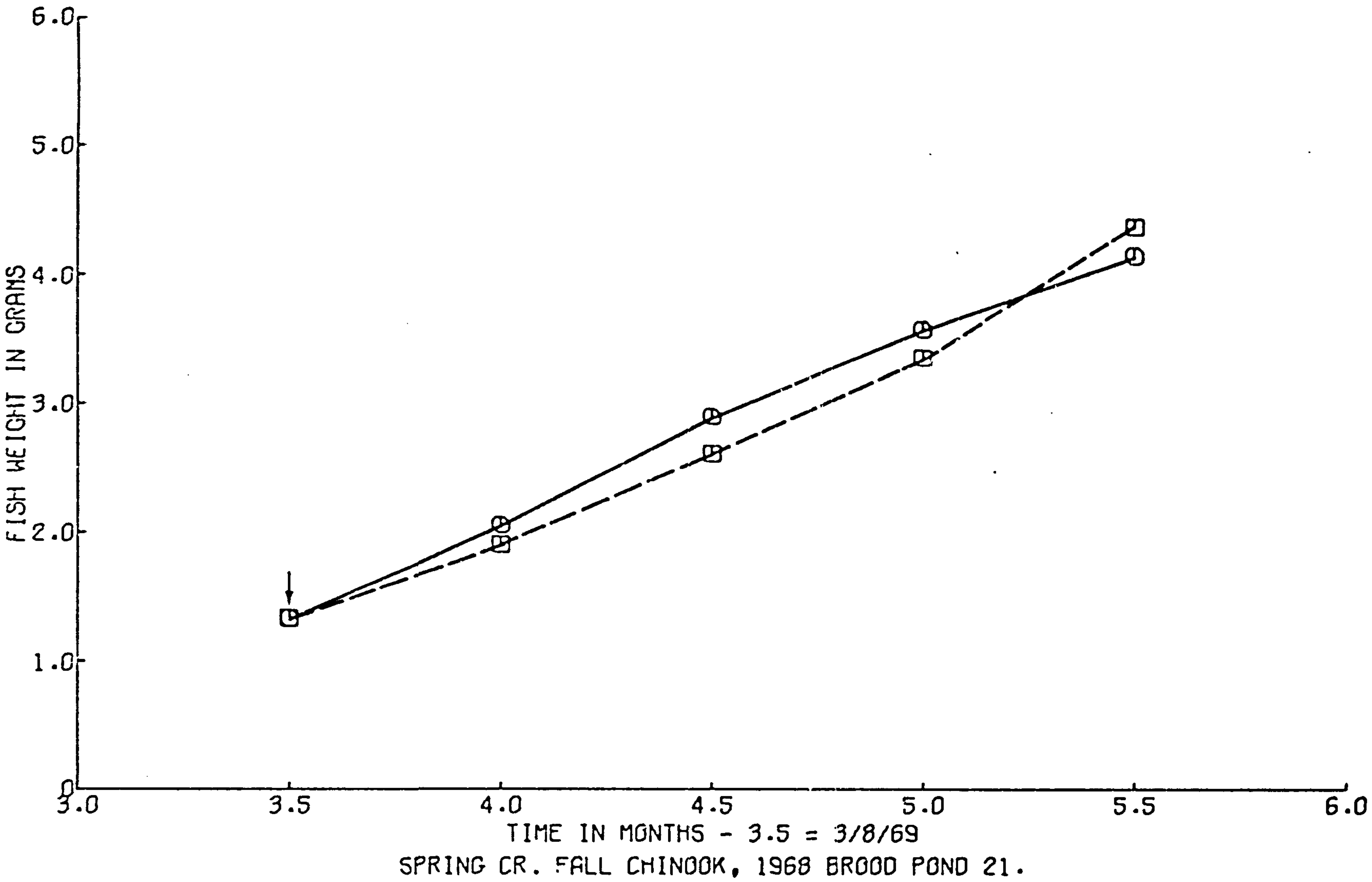


FIGURE 23. The observed (——) and the simulated (---) growth of the fall chinook salmon from the 1968 Spring Creek brood reared in pond 21 of the WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).

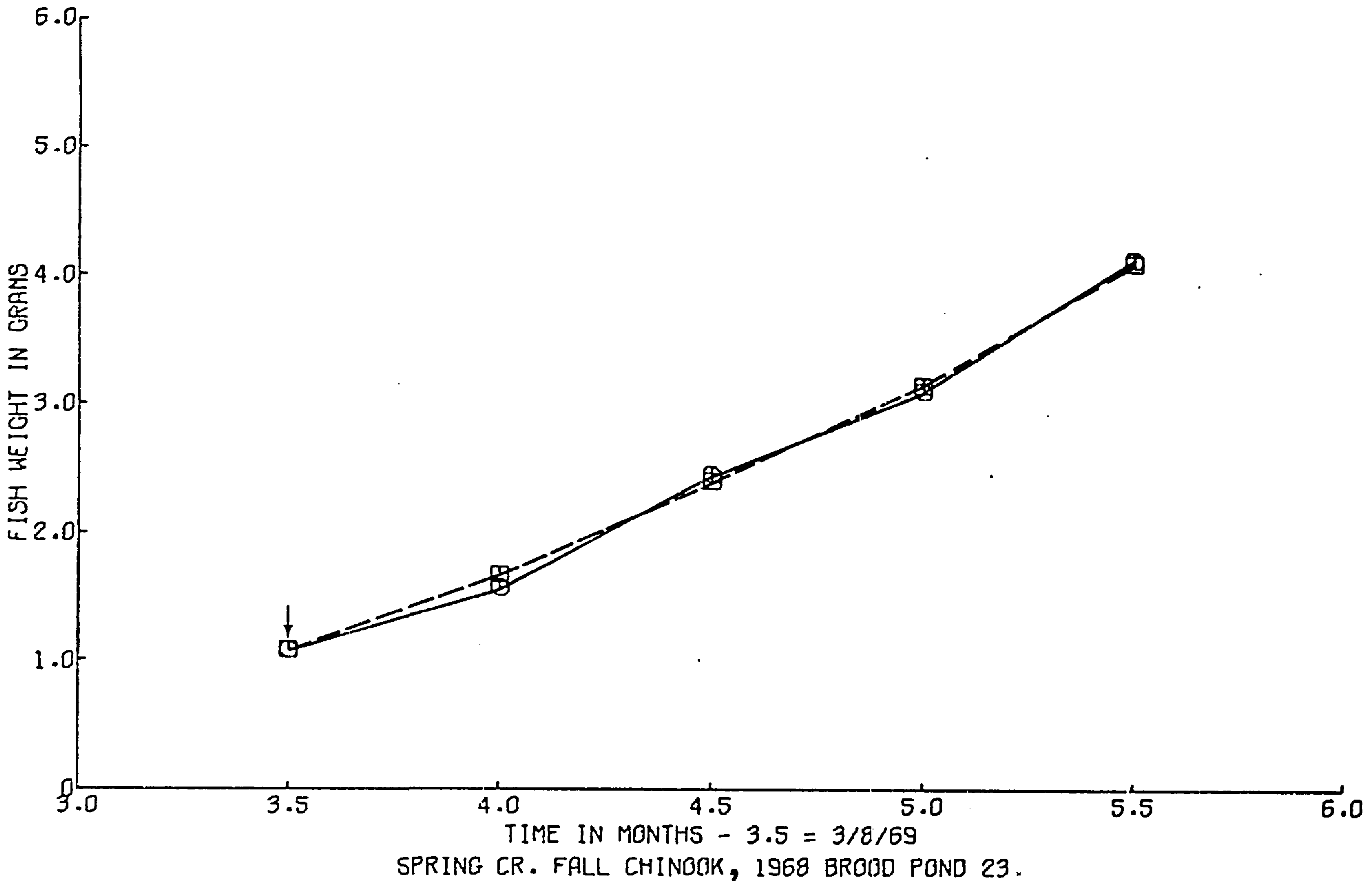


FIGURE 24. The observed (——) and the simulated (---) growth of the fall chinook salmon from the 1968 Spring Creek brood reared in pond 23 of the WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).

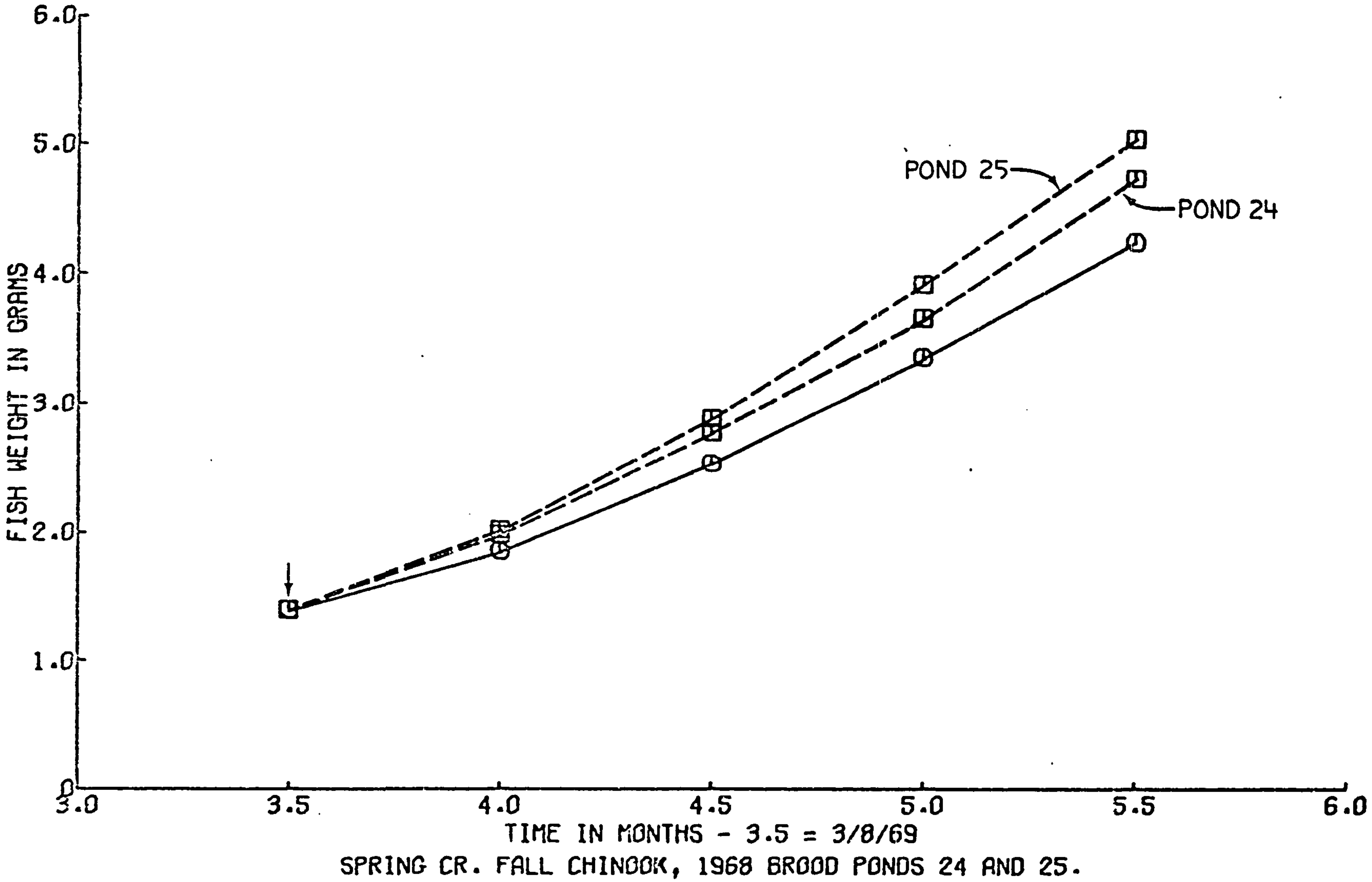
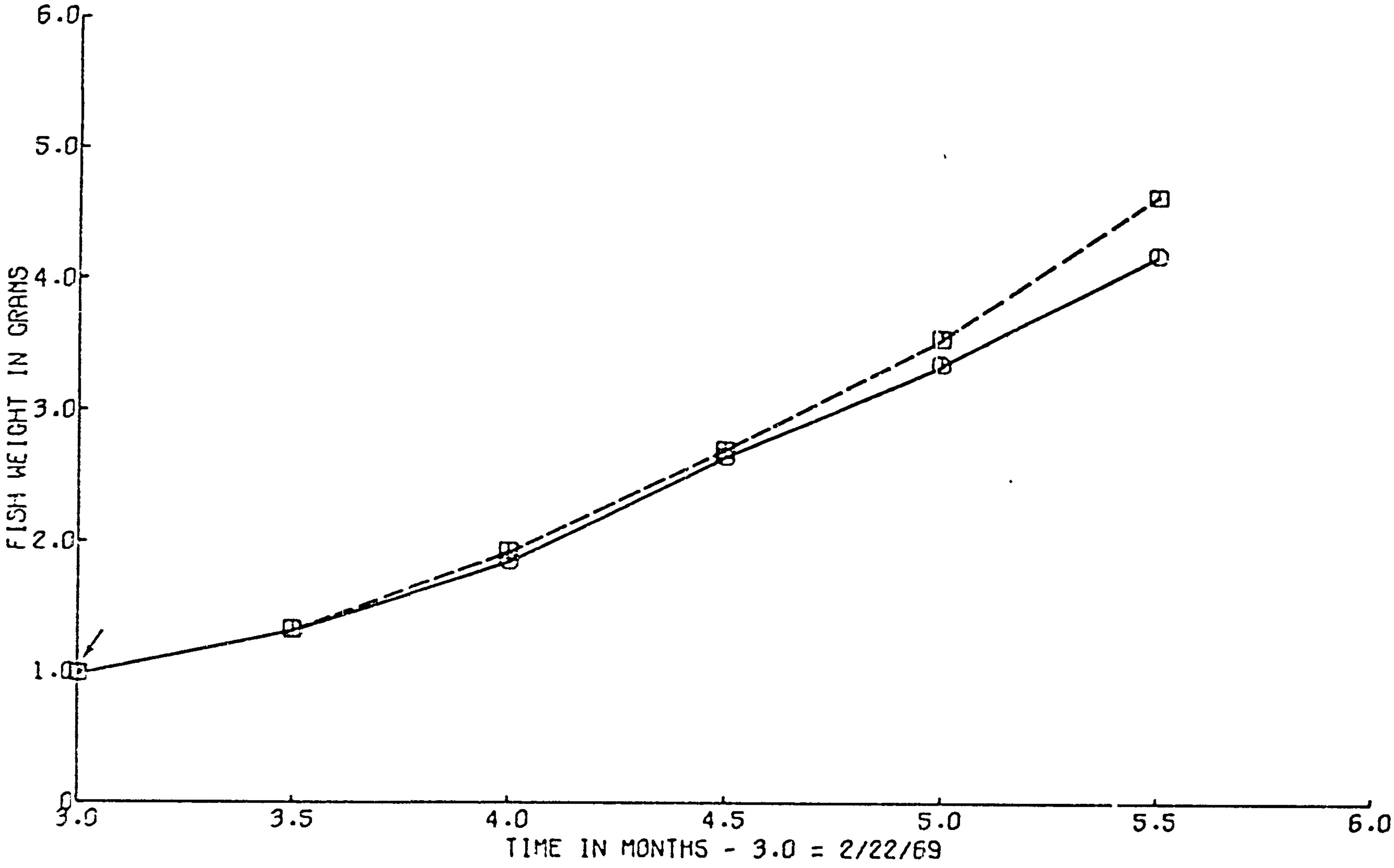


FIGURE 25. The observed (——) and the simulated (---) growth of the fall chinook salmon from the 1968 Spring Creek brood reared in ponds 24 and 25 of the WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).



SPRING CR. FALL CHINOOK, 1968 BROOD. ALL PONDS COMBINED.

FIGURE 26. The observed (——) and the simulated (---) growth for the entire lot of fall chinook salmon from the 1968 Spring Creek brood reared at the WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).

water temperature is greatly reduced compared to the temperatures of other hatcheries. Second, the comparison of the simulations between ponds points out the influence of daily rations in the predicted specific growth rates. Third, the simulation predicts the growth for the individual ponds and the entire lot about equally as well.

Green River and Minter Creek hatcheries

Fall chinook lots were also selected from the WDF Green River and Minter Creek hatcheries, where the water temperatures undergo more pronounced daily and seasonal cycles. Four lots from the Green River hatchery provide comparisons of the growth of fish from an early hatch date with those from a later date. In addition, two Green River lots and two Minter Creek lots provide comparison of versions of the Oregon and Abernathy diets. Also included are Finch Creek fall chinook salmon that were reared at the Minter Creek hatchery during the summer of 1969 to a size of 20 grams.

The hatching period for salmon eggs from the same stock hatch may extend over a month or more. Separate records for lots from the early and late hatches could be identified for the 1969 and 1970 brood reared at the Green River hatchery. The growth of the fish in the late hatch is usually accelerated compared to the fish in the early hatch. The reason is that the late fish usually experience warmer water temperatures earlier in life and, therefore, can consume higher rations earlier.

Approximately 280,000 fall chinook salmon from the early hatch of the 1969 brood were placed in the rearing ponds on 17 January 1970. A similar number of fish from the late hatch were ponded almost a month later on 14 February. In the first week of April half of each lot was planted as pre-smolts. The remaining fish in the early lot were reared until 14 May 1970 and the remaining fish in the late lot were planted 12 days later on 26 May 1970. The average water temperatures during this time steadily increased from 5 to 10°C (41 to 50°F). Both lots received Oregon pellets once they outgrew the starter diets.

The results of the simulations of these lots are shown in Figure 27 and are listed in Table 2 of Appendix II. The simulations were started on 21 February (month 3.0) for the early lot when the fish averaged 0.685 grams and on 7 March (month 3.5) for the late lot when fish averaged 0.600 grams. Both simulations were terminated on 16 May (month 6.0). The predicted weights for both lots were similar to the recorded weights up to the time of the pre-smolt plant (month 4.5). Beyond this time the predicted greatly exceeded the observed. The records show that the fish in both lots grew about 1 gram in the last half of month 4. On the other hand, the simulation predicted a 0.5 gram increase in weight for both lots. The simulation also predicted that the average daily ration fed during this two week period exceeded the maximum ration. If the data are correct then the fish obviously took advantage of the high ration. This suggests that the maximum ration and the maximum specific growth rate

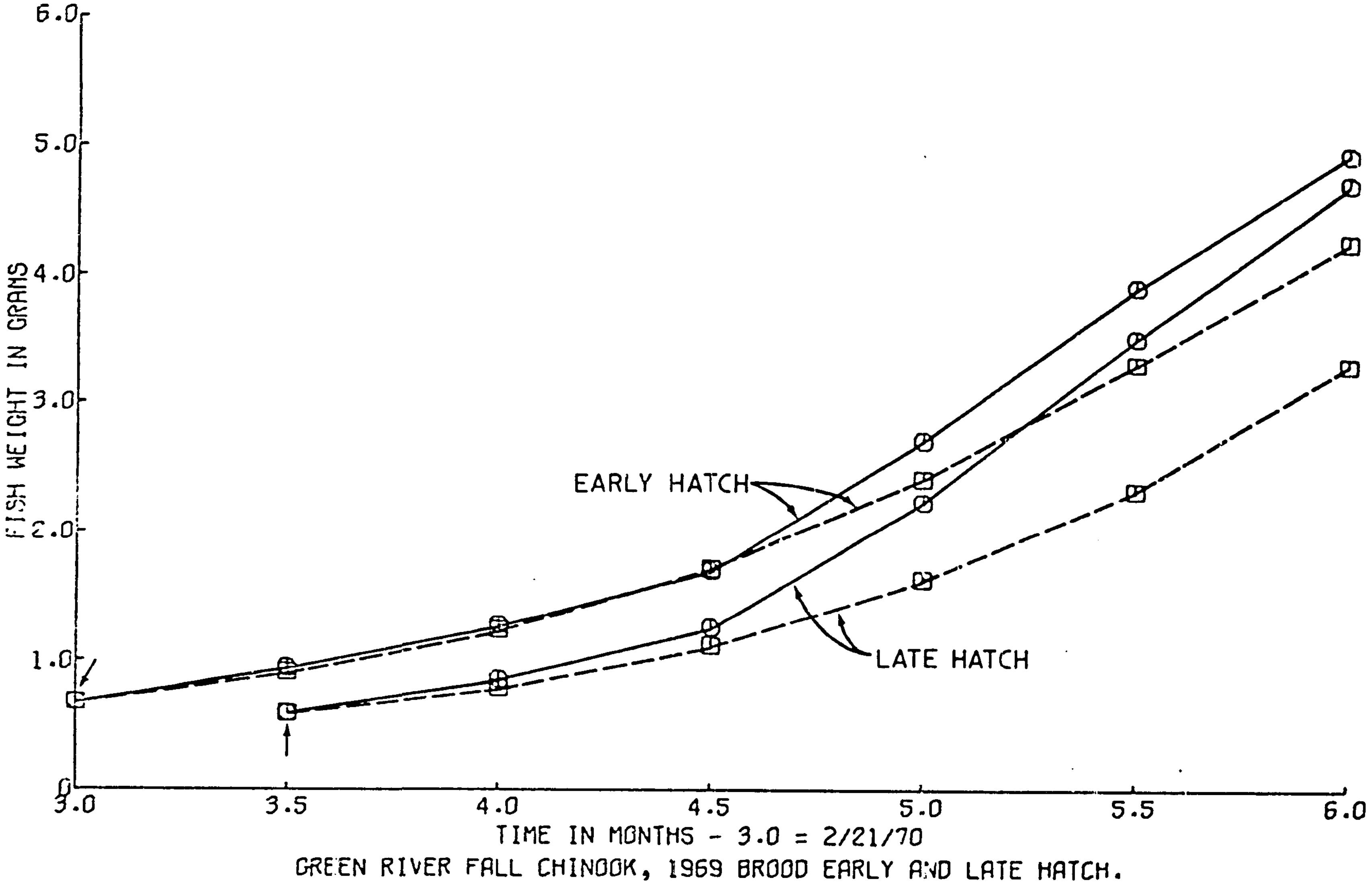


FIGURE 27. The observed (——) and the simulated (---) growth for the early and late lots of fall chinook salmon from the 1969 brood reared at the WDF Green River hatchery, the shorter arrows indicate the start of the simulation (1 month = 28 days).

expressions might be in error. Other possible causes could be that after the pre-smolt plant the actual number of fish on hand was less than recorded. This would have the affect of increasing the daily ration above the calculated value. Also there is a small possibility that the pre-smolt plant released a greater proportion of the smaller fish. This would bias the growth rate upward.

The simulation of the growth for similar lots from the 1970 brood is considerably better as shown in Figure 28 and Table 3 of Appendix II. The early lot was ponded on 2 February 1971, and the late lot 17 days later. Both lots started with about 275,000 fish and both were fed the Oregon starter mash for two weeks and Oregon pellets thereafter. As in the year before, both lots were evenly split in mid-April. The dates of the final plant were 19 May for the early lot and 1 June for the late lot. The simulations were started on 6 March (month 3.5) for the early and late lots when the fish averaged 0.738 grams and 0.575 grams respectively. They were terminated on 15 May 1971 (month 6.0). The predicted weights are almost exactly the observed for the late lot and just slightly lower than the observed for the early lot. The average daily rations were close to but never exceeded the estimate of the maximum daily ration. Neither the daily rations nor the observed growth took a jump after the mid-April split.

Another group of fish from the 1970 early hatch lot were reared in a pond at the Green River hatchery but these were fed the Moore-Clark Abernathy dry diet. Also the number of fish in the pond was about half the usual number. On the planting

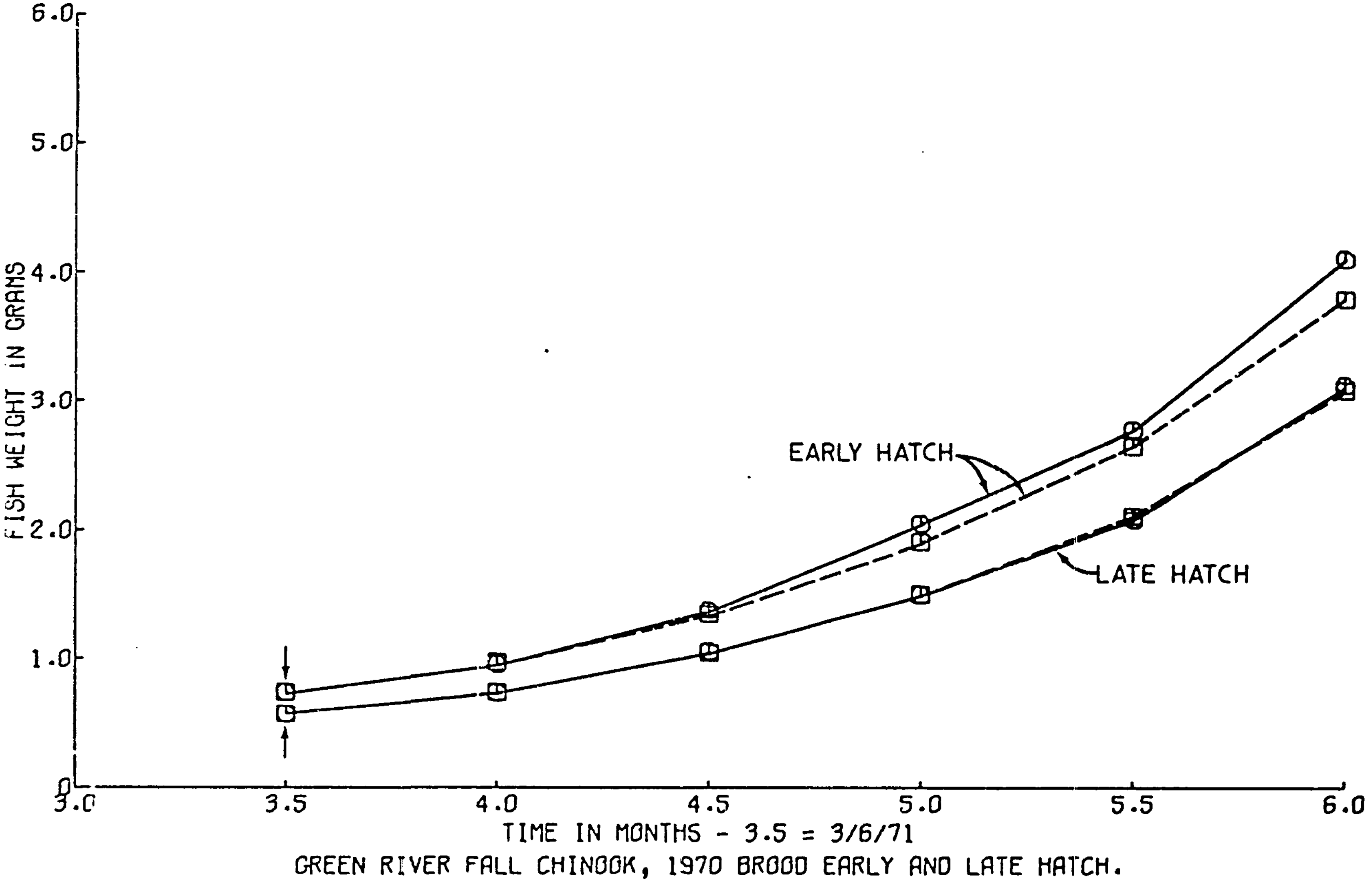


FIGURE 28. The observed (——) and the simulated (---) growth for the early and late lots of fall chinook salmon from the 1970 brood reared at the WDF Green River hatchery, the shorter arrows indicate the start of the simulations (1 month = 28 days).

day, 19 May 1971, it was determined that the pond contained 10,000 more fish than the 84,000 in the inventory records. To correct for this overage, 10,000 fish were added to each weekly inventory.

The results of the simulation of this lot are shown in Figure 29 and in Table 3 of Appendix II along with the previous results for the early lot fed the Oregon diet. The time spanned by the simulation is identical for both diet groups, but the average size of .700 grams for Abernathy groups at the start is slightly less than the Oregon group. The average daily rations for the Abernathy group are between 65 and 70% of the amount for the Oregon group. Yet the model slightly underestimated the growth for both groups by almost equal amounts. The assumption that the moisture content of food was 32% for the Oregon diet and 10% for the Abernathy diet accounted for the major portion of the differences between the daily rations. The differences in growth of the two groups is probably due to the differences in starting size or the slight differences in dry weight feeding levels rather than differences in diets because the simulator performed about equally as well for the two groups without changing the coefficients of the growth equation other than FDMCT. The final size of 3.31 grams for the Abernathy group was only increased to 3.39 grams by altering FDMCT to 8%.

The comparison of two other diet trials indicates that the growth potential for two similar diets was different. In this case the fish were from the 1968 brood reared at the Minter

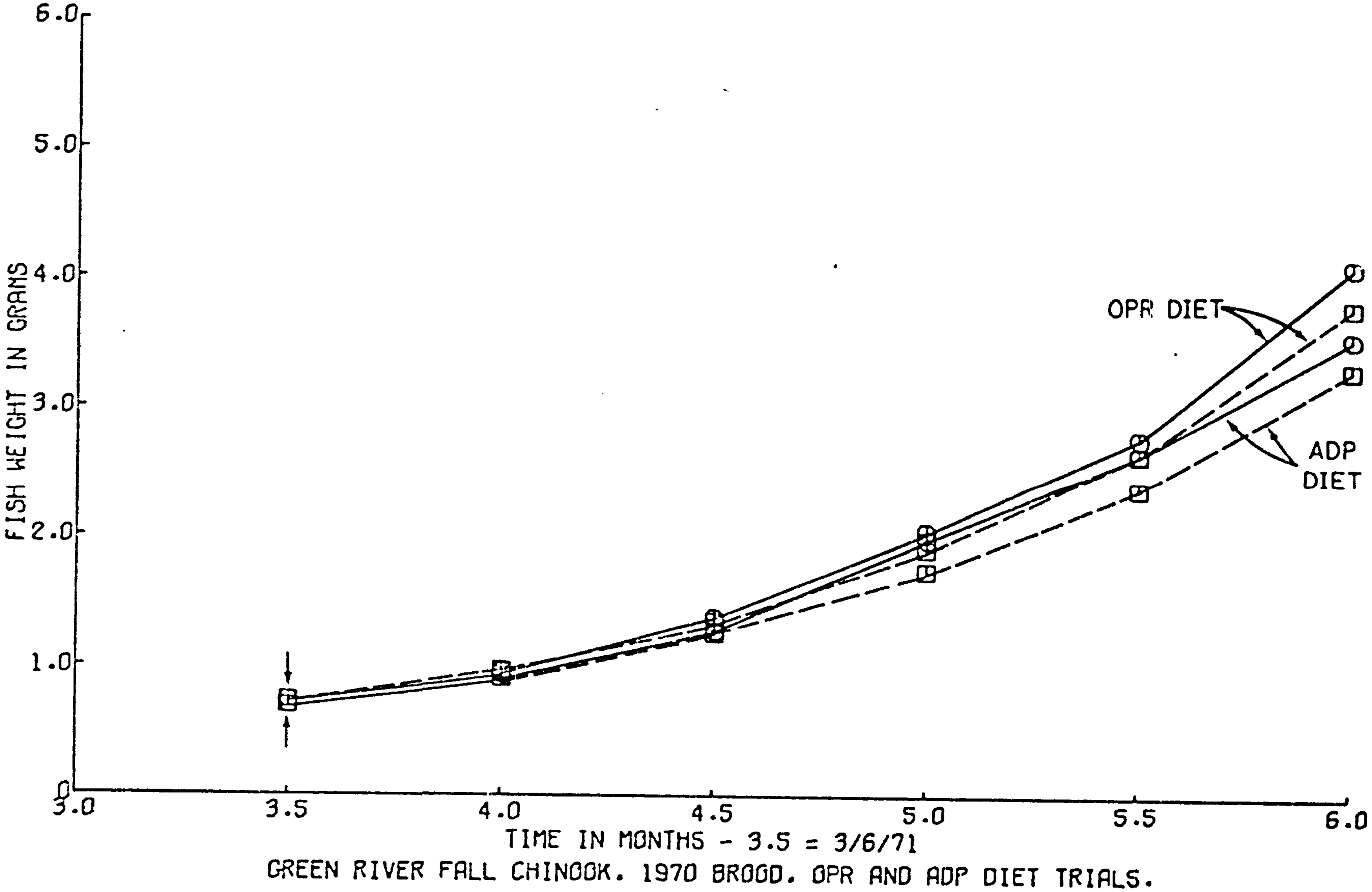


FIGURE 29. The observed (——) and the simulated (---) growth for two trial lots of fall chinook salmon from the 1970 brood reared at WDF Green River hatchery and fed an Oregon or an Abernathy diet, the shorter arrows indicate the start of the simulation (1 month = 28 days).

Creek hatchery. The two lots were part of a diet experiment conducted by Westgard (1969 MS). Both lots were placed in rearing ponds on 21 March 1969. One lot was initially fed Ellis mash and switched on 19 April to an Oregon pellet with a herring oil substitute. The other lot was put on the Abernathy starter ans switched on 19 April to an Abernathy pellet diet with a whey substitute. The first lot started with 500,000 fish and was eventually reduced to 10,000 by the end of the experiment. The second lot began with 50,000 fish and was cut once to around 27,000. Both lots were planted on 23 June 1969. Average water temperatures steadily increased from 9.7 to 13.3°C (49.5 to 56°F) during this period.

The simulations were started on 19 April (month 5.0) for the lot fed the Oregon diet and 5 May (month 5.5) for the other lot. The initial average weights were 0.78 and 1.08 grams respectively. Simulations beginning on earlier dates produced below normal growth for the early weeks for both lots. Both simulations were terminated 14 June (month 7.0). The simulation results are shown in Figure 30 and listed in Table 4 of Appendix II. The simulation predicted that the average fish weights for both lots were almost equal to the average weights recorded for the Abernathy lot. The simulated weights for the Oregon lot were made equal to the observed weights by increasing the coefficient a_6 from the standard 0.0383 to 0.0460. The greater growth of the Oregon lot cannot be attributed to differences in initial sizes or feeding levels. These results suggest that the "scope of growth"

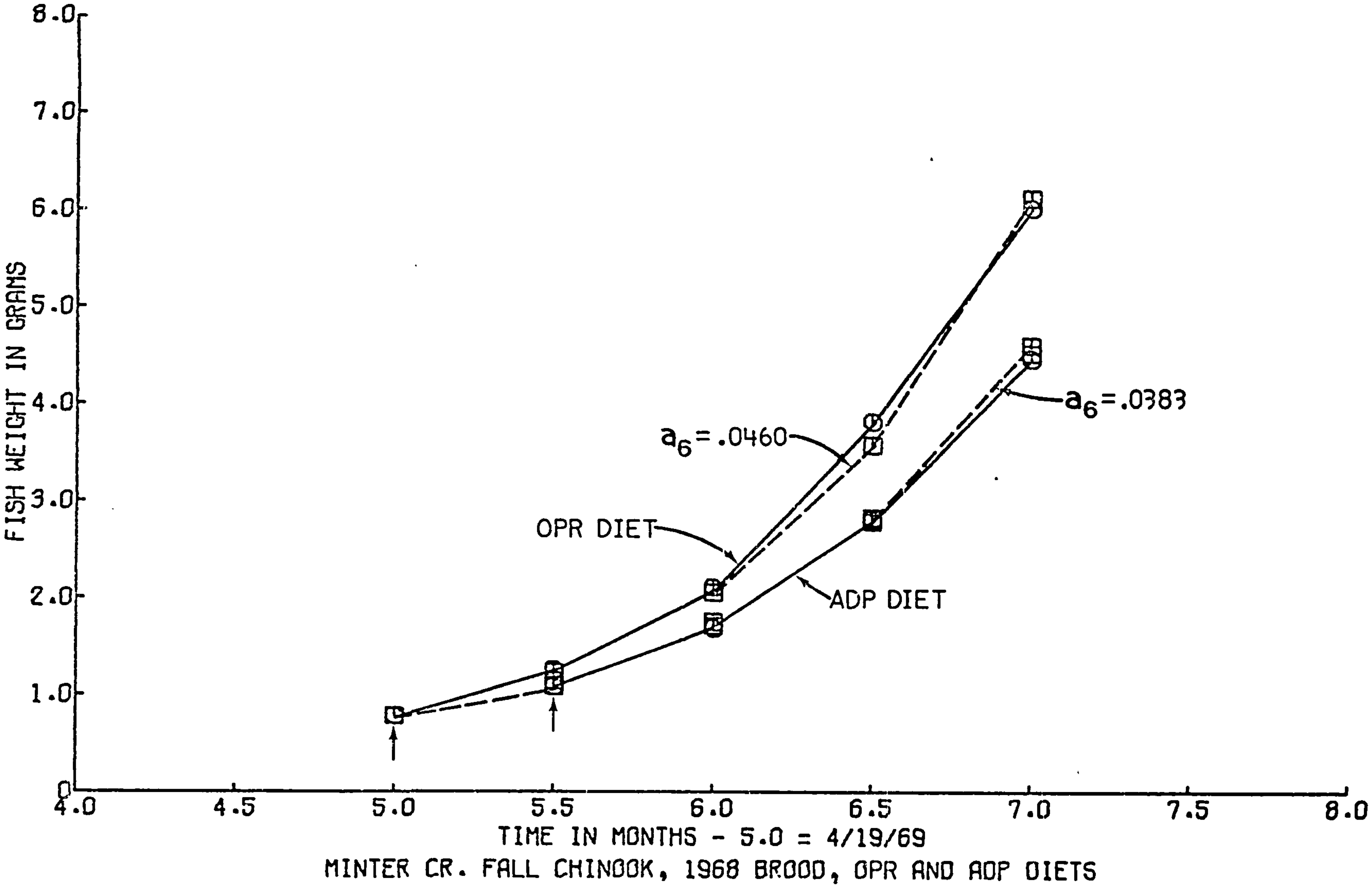


FIGURE 30 The observed (——) and the simulated (---) growth for the two trial lots of fall chinook salmon from the 1968 brood reared at WDF Minter Creek hatchery and fed an Oregon diet (with a_6 = .0383 or .0460) or an Abernathy diet (with a_6 = .0383), the shorter arrows indicate the start of the simulation (1 month = 28 days).

of the modified Oregon diet was indeed greater than that of the modified Abernathy diet. This conclusion should be qualified until the behaviour of the growth model is better understood and the accuracy of the input data is confirmed. These two pairs of simulations though do demonstrate the application of the growth model in comparing diet trials where important variables such as initial size, water temperatures, or daily rations are not consistent between trials.

The final lot of fall chinook salmon to be presented are from the 1968 Finch Creek brood. A total of 100,000 were transferred from the WDF Dungeness hatchery to the Minter Creek hatchery on 2 June 1969 at an average size of 0.73 grams. The lot was split evenly into three ponds to test three preparations of the Oregon pellet diet. The experiment was terminated on 9 August 1969, but the fish were held at the hatchery until 31 October 1969. On 1 August the entire lot was reweighed and it was determined that there were 12,200 fish less than previously recorded. In mid-September the entire lot was counted and marked. The count showed that there were 8,400 more fish than previously recorded. All the previous inventory records were adjusted to agree with the final count. The average water temperatures during the diet experiment varied slightly around 11.6°C (53.0°F). After the experiment the temperatures steadily dropped to about 7.2°C (45°F).

For simulation purposes the three ponds were combined and treated as one since the same estimate of fish size was recorded for all three ponds after the end of the diet experiment.

The simulation was started on 14 June (month 7.0) when the fish averaged 1.05 grams and was terminated 1 November 1969 (month 12.0) one day after the fish were planted when they would have supposedly averaged 20.75 grams. The simulated weights paralleled the observed average weights up to month 9.0 which corresponds to the end of the experiment (see Figure 31 and Table 5 of Appendix II). The observed weight for the end of the second week of month 9.0 took a large jump that was not predicted by the simulation. A restart of the simulation on 9.5 when the fish averaged 10.2 grams produced a growth curve similar to the observed. Except for the one two week period following the end of the experiment, the growth model performed quite well for both the smaller and larger sized fish.

Results for spring chinook salmon

The 1968 brood spring chinook salmon reared at WDF Klickitat hatchery provide further opportunities to test the growth model for chinook salmon larger than 5 grams. The hatch totalling 0.5 million fry was placed in ponds on 7 January 1968. They were fed Ellis starter mash and Oregon pellets. During the first half of June the fingerlings were graded into three size categories. The smaller fish averaged 2.6 grams and filled one pond. The medium sized fish filled 5 ponds and averaged 3.45 grams. Only the records for pond 9 were processed for simulation. The larger fish averaged 5.38 grams and were put in one pond. The 84,000 fish in the small category were split and placed into two ponds in the first week of August. During

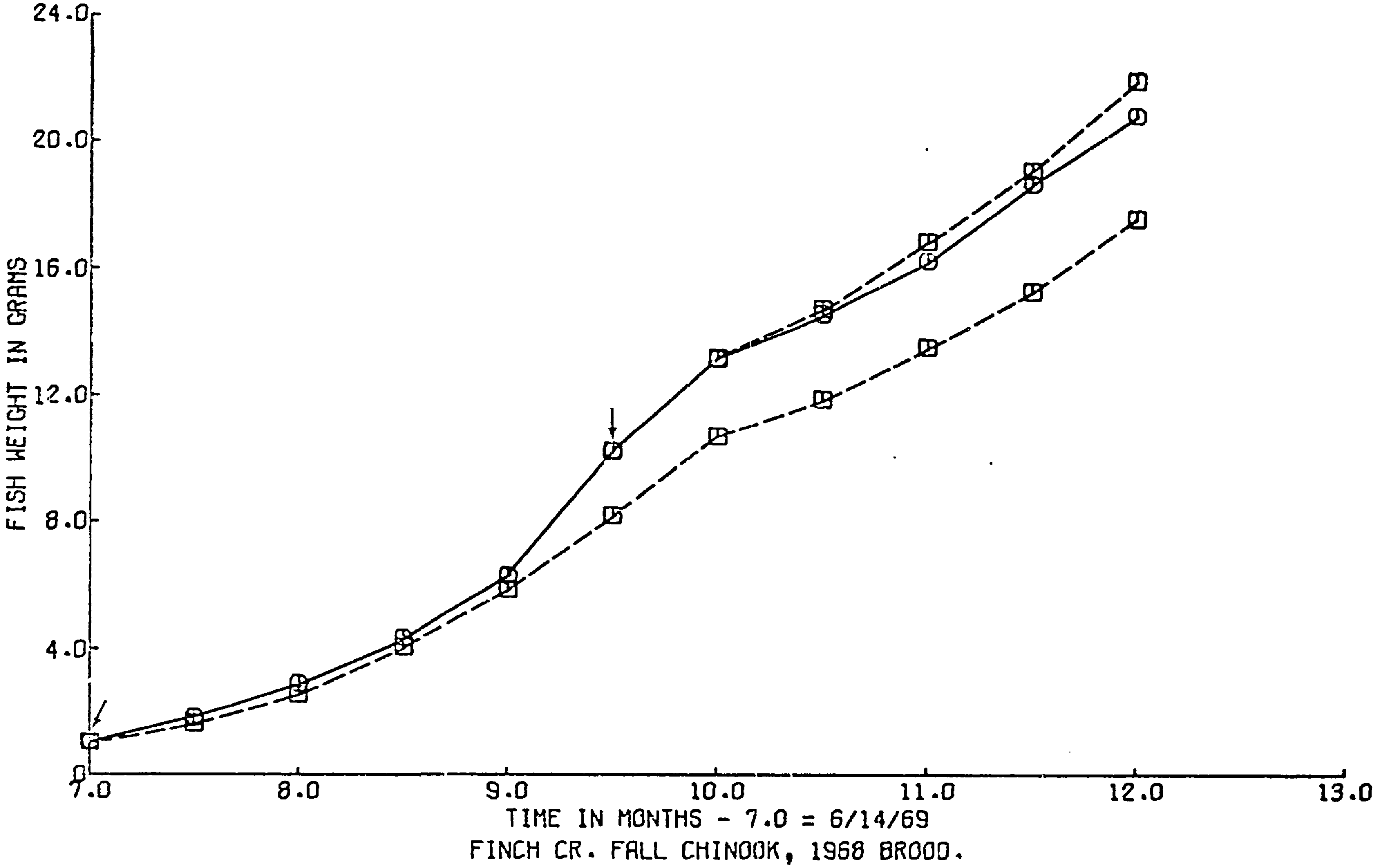


FIGURE 31. The observed (——) and the simulated (---) growth of the fall chinook salmon from the 1968 Finch Creek brood reared through the summer at WDF Minter Creek hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

that same time the 65,000 fish in pond 9 were cut to 43,000. The identity of the small lot was lost on 27 December 1969 when it was mixed with other fish in a larger production pond. The same happened to the fish in pond 9 on 31 January 1970. The 45,000 fish in the large category remained in their original pond until they were planted on 18 March 1971.

The simulation results for these three lots are displayed in Figures 32, 33, and 34 and are listed in Table 6 in Appendix II. The starting date was 14 June (month 7.0) for the fish in the two smallest size categories and two weeks later (month 7.5) for the large grade lot. The simulations were terminated on 27 December 1969 (month 14.0) for the small grade lot, 17 January 1970 (month 14.5) for the medium grade lot, and 21 March 1971 for the large grade lot. This latter date is three days after the fish were planted. The growth of the small grade lot was slightly underestimated during the first three months of simulation. But by 10.5 the predicted values were almost identical to the observed weights. For the weeks after 11.5 the predicted weights exceeded the observed by an increasingly wider margin. This same general pattern occurred for the simulation of the medium grade lot. In this case, though, the deviations were greater. The average fish sizes recorded after 18 October (month 11.5) were identical for the medium and large grade lots. This leads to the conclusion that the observed weights might not be accurate. The simulation of the large grade lot produced more consistent results. For the first 3 months, this lot was fed at a level

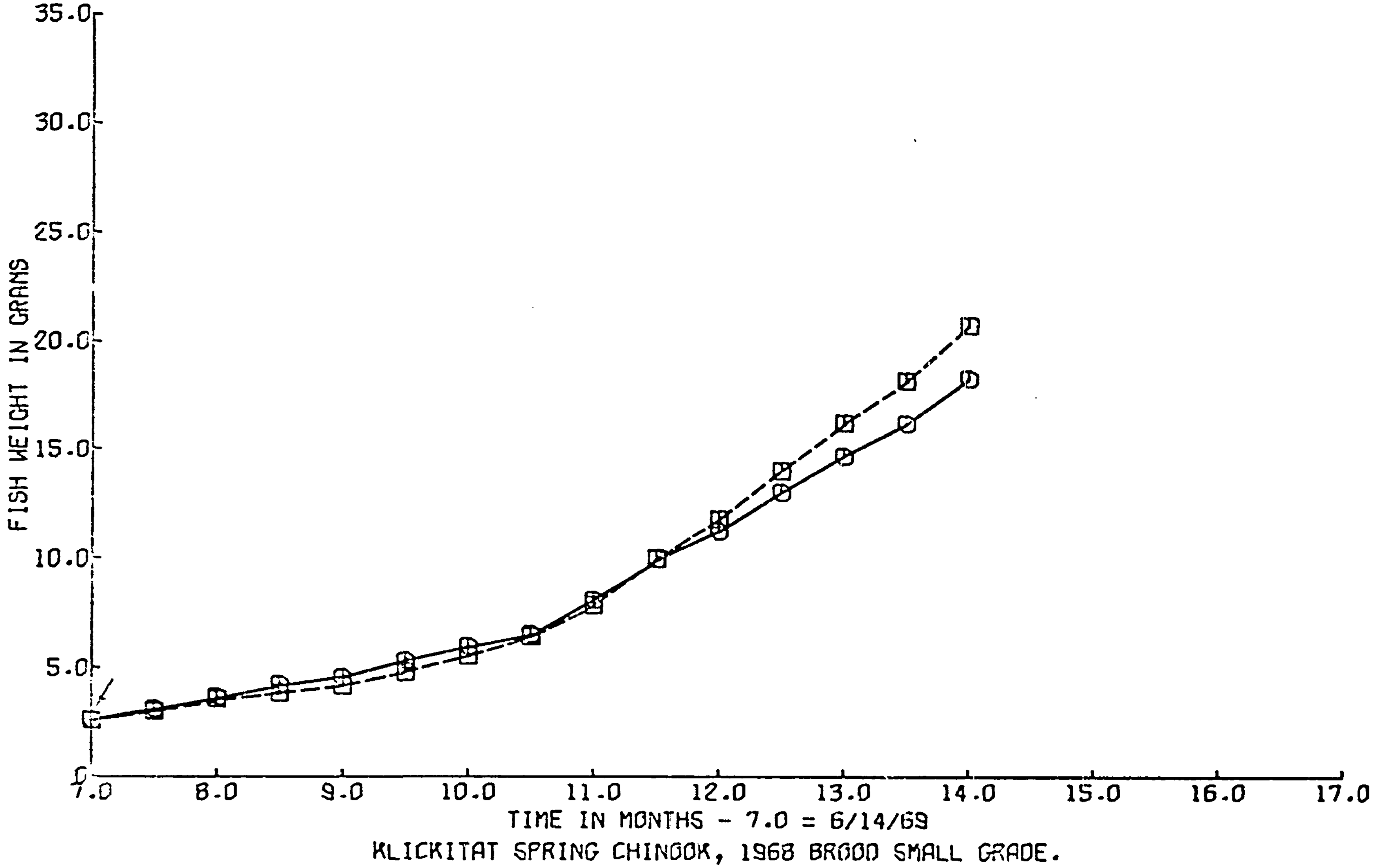


FIGURE 32. The observed (——) and the simulated (---) growth for the small grade lot of spring chinook salmon from the 1968 brood reared at WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).

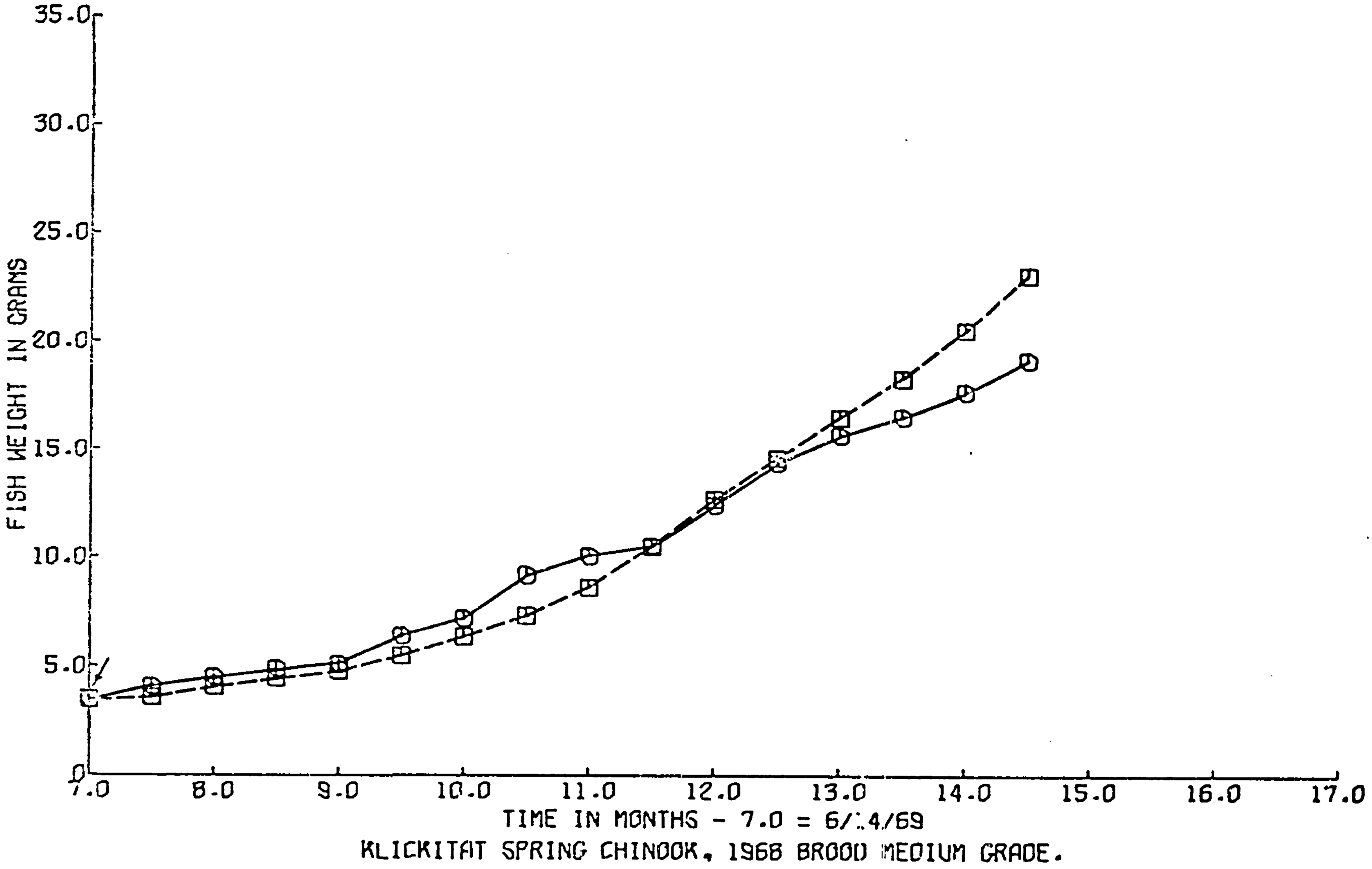


FIGURE 33. The observed (——) and the simulated (---) growth for the medium grade lot of spring chinook salmon from the 1968 brood reared at WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).

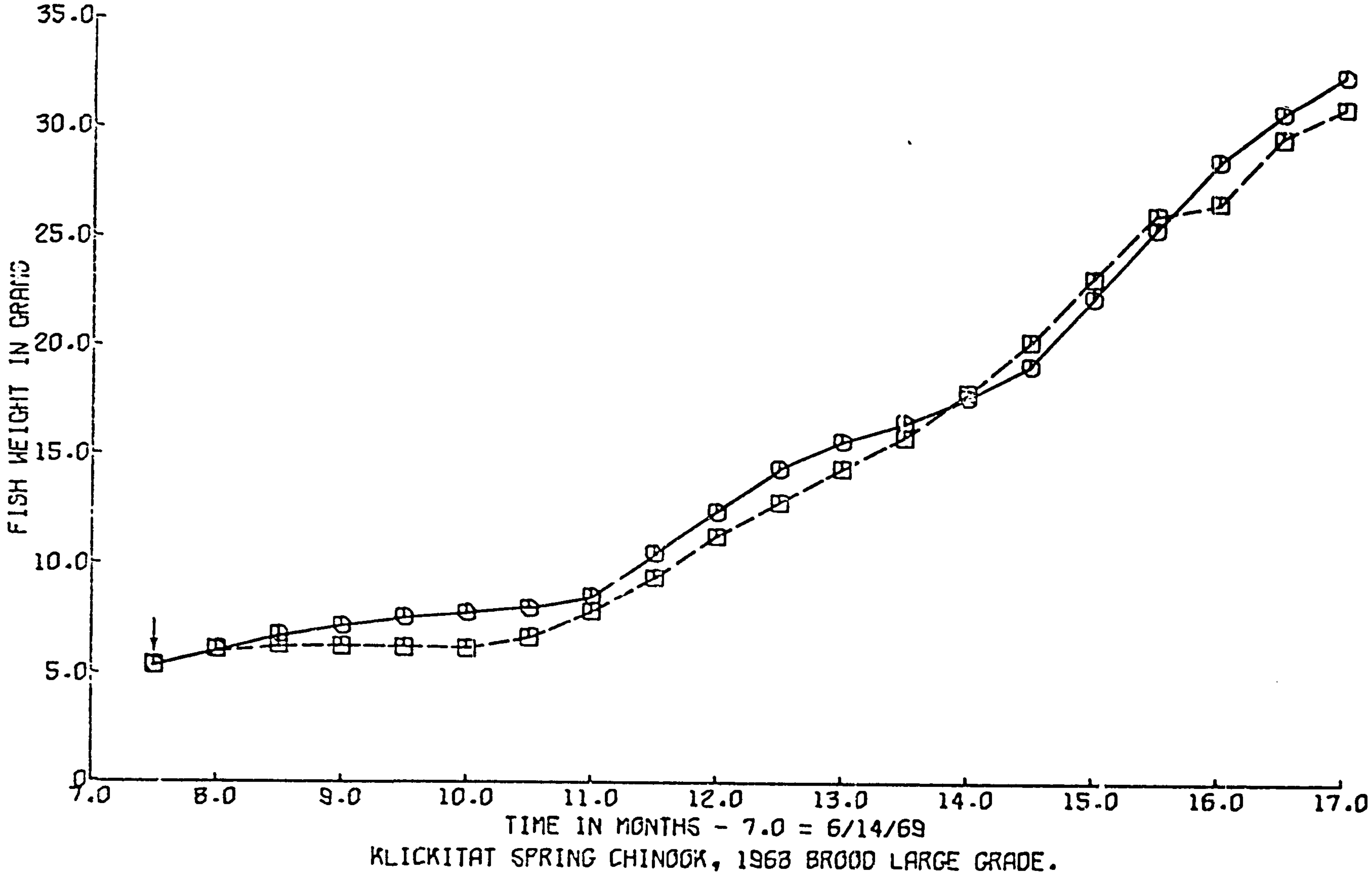


FIGURE 34. The observed (——) and the simulated (---) growth for the large grade lot of spring chinook salmon from the 1968 brood reared at WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).

slightly above maintenance to slow down their growth rate. The predicted maintenance rations though were slightly greater. Consequently the predicted growth rates were lower than the observed rates. An increase in ℓ_3 or a decrease in ℓ_4 would correct this. After the ration levels were increased, the simulated growth increased and surpassed the observed values. During the last two weeks of month 15, the observed rations were relatively low and the simulator responded with a low rate of growth. This caused the predicted weights to fall below the observed. Although some discrepancies exist in these simulations, in general the simulations predicted the growth quite well for the three sets of circumstances.

Results for coho salmon

Klickitat hatchery

The coho salmon reared at the WDF Klickitat hatchery, like the fall and spring chinook salmon, are good for testing the growth model. The lot from the 1968 brood had a history similar to the spring chinook discussed earlier. Over one million fry were ponded on 7 January 1969. They were fed Ellis and Abernathy starter diets and Oregon pellet production diets. The fish were graded into four size groups in the first week of June. The very small grade lot consisted of one pond with 68,000 fish averaging 1.32 grams each. The small grade lot filled five ponds each containing about 75,000 fish weighing 2.21 grams on the average. The 220,000 fish in the large grade lot were split evenly into three ponds. They averaged 3.27 grams per fish. The extra large lot contained only 23,000 fish but they averaged 4.88 grams.

The simulations for the four lots were started on 14 June 1969 (month 7.0) and stopped on 22 November 1969 (month 12.5) just before all the fish were transferred to one large production pond. The average weights for the four lots at the start of the simulations were 1.58, 2.66, 3.70, and 5.68 grams. The small and large grade lots were included in the data sets used in the optimization of ℓ_3, ℓ_4, and a_6. The initial simulations for the extra large lot surprisingly indicated that the estimated values of the maintenance rations were too high. The value of ℓ_3 was lowered from 0.0321 to 0.0240 to increase the predicted growth during periods of low feeding levels. This new value is almost the same as the original estimate derived from the literature.

The initial simulation of the very small lot also produced unsatisfactory results. These fish generally grew slower than predicted. For the majority of the weeks, though, the daily rations were double those of the other three groups (see Table 7 in Appendix II). Based on the evidence given by Brett, et.al. (1969), the moisture content of the fish flesh may be lower for the very small lot than for the other three groups. A decrease in FHMCT from 0.75 to 0.72 greatly reduced the discrepancies between the predicted and observed weights as shown in Figure 35. An alternative approach might be to decrease a_6 and possibly to increase ℓ_3. This would have the affect of reducing the

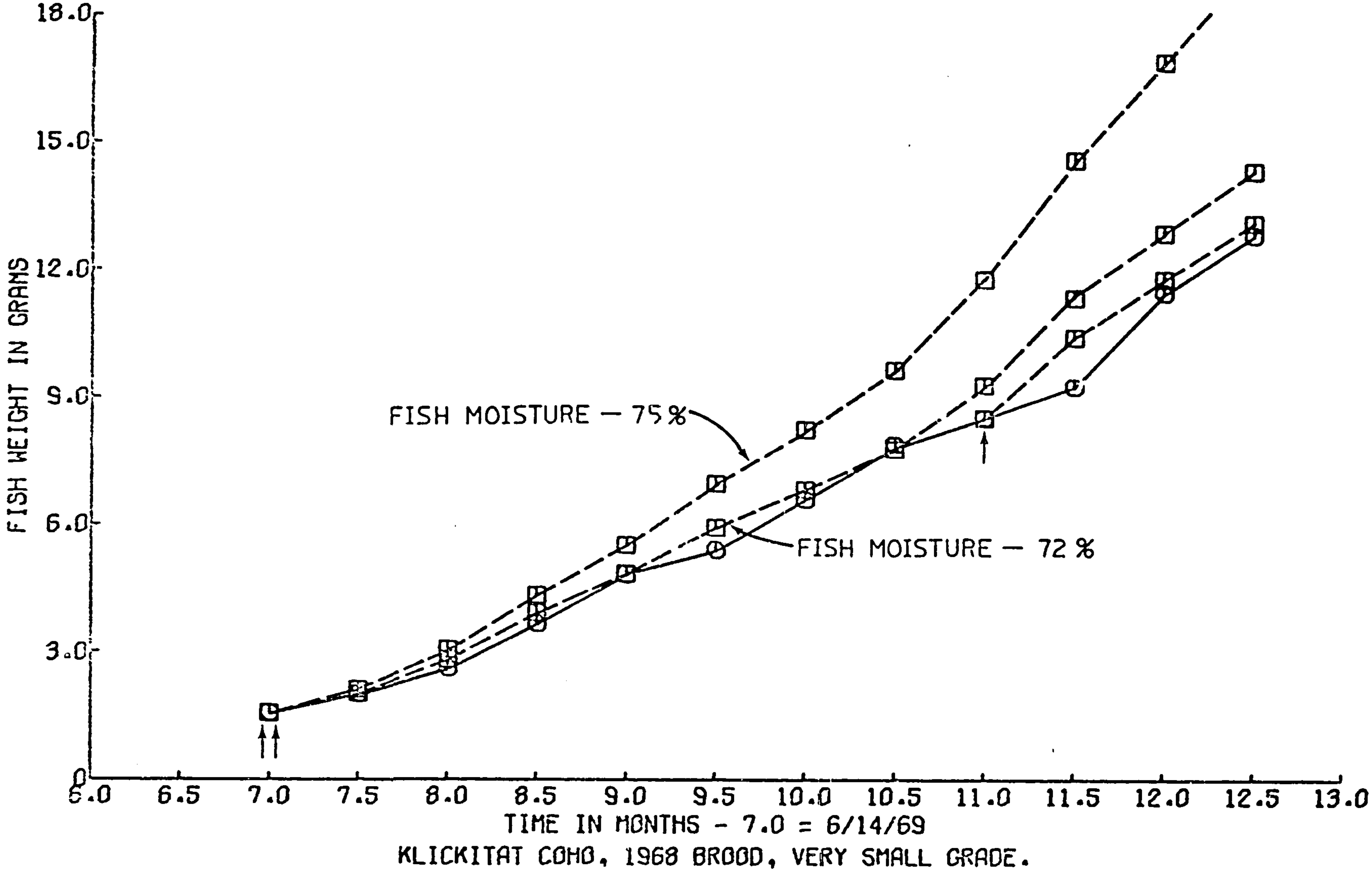


FIGURE 35. The observed (——) and the simulated (---) growth for the very small grade lot of coho salmon from the 1968 brood reared at the WDF Klickitat hatchery, the shorter arrows indicate the start and restart of the simulation (1 month = 28 days).

"scope for growth" of these fish. This can be justified by the fact that the fish in this lot were selected on the basis of slow growth.

The simulation for the small grade lot (Figure 36 and Table 7 in Appendix II) with FHMCT = 0.75 produced a growth pattern almost identical to the observed except after month 10. In the last six weeks the simulated weights exceeded the observed weights. The probable cause for the discrepancies cannot be found but the pattern of the discrepancies is similar to that for the small and medium grade lots of Klickitat spring chinook. The simulator consistently underestimated the growth of the large lot (Figure 37). The simulation results were somewhat improved by restarting it on 7.5. A similar pattern occurred for the simulation of the extra large grade lot except for the middle two months where the discrepancies were greater (Figure 38). The discrepancies were reduced by restarting the simulation on 8.0. The first three months of simulation of the four lots demonstrate the models ability to predict the growth of fish of different sizes on different feeding schedules.

Minter Creek hatchery

The simulation of coho salmon from the WDF Minter Creek hatchery tests the growth model for this species reared in an environment with fluctuating temperatures. A coho lot from the 1968 White River stock was selected for one of the tests. This lot was included in data set 1 for the coefficient optimization routine. The lot, totaling 144,000 fish, was placed in

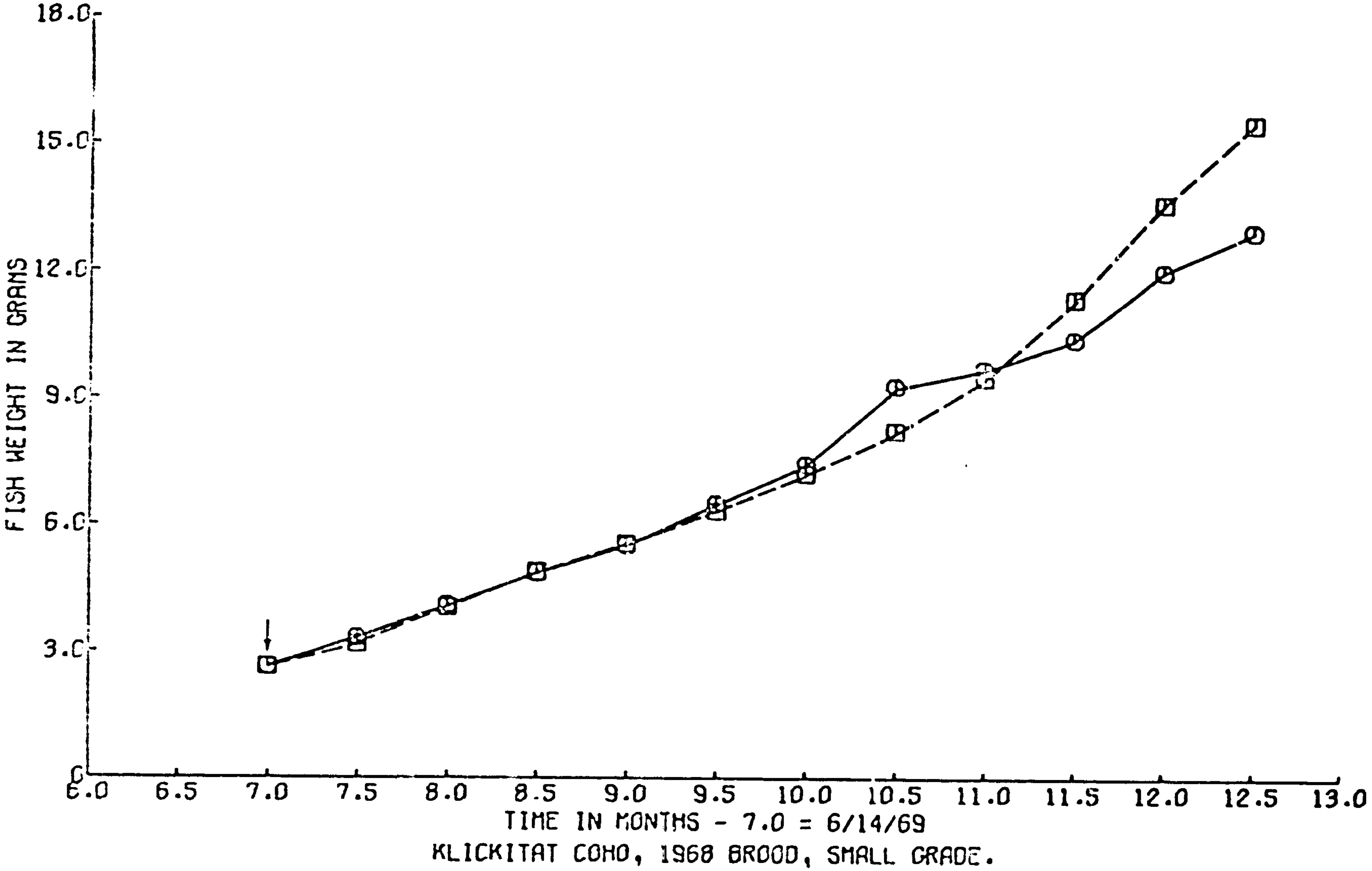


FIGURE 36. The observed (——) and the simulated (---) growth for the small grade lot of coho salmon from the 1968 brood reared at the WDF Klickitat hatchery, the arrow indicates the start of the simulation (1 month = 28 days).

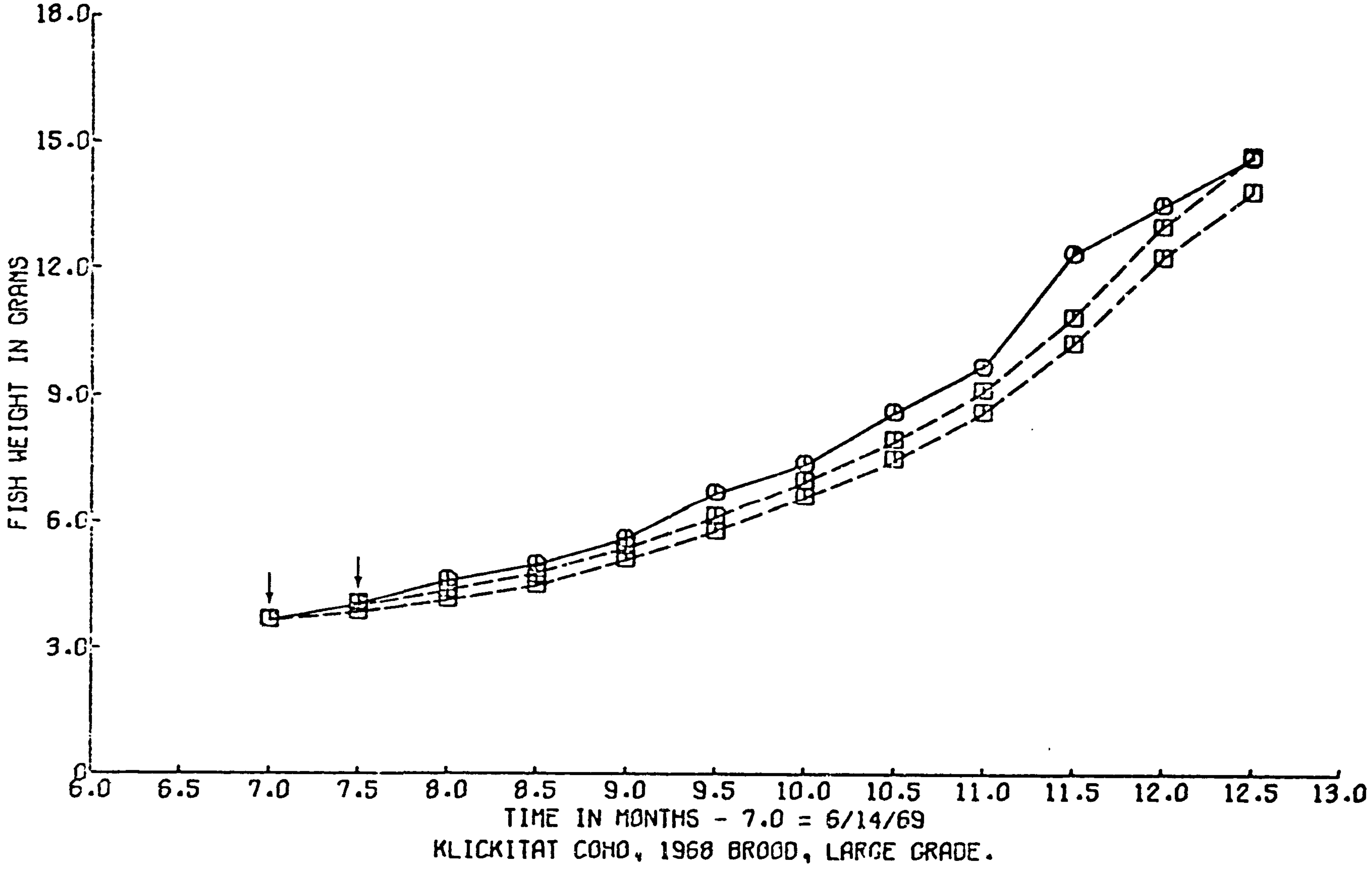


FIGURE 37. The observed (——) and the simulated (---) growth for the large grade lot of coho salmon from the 1968 brood reared at WDF Klickitat hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

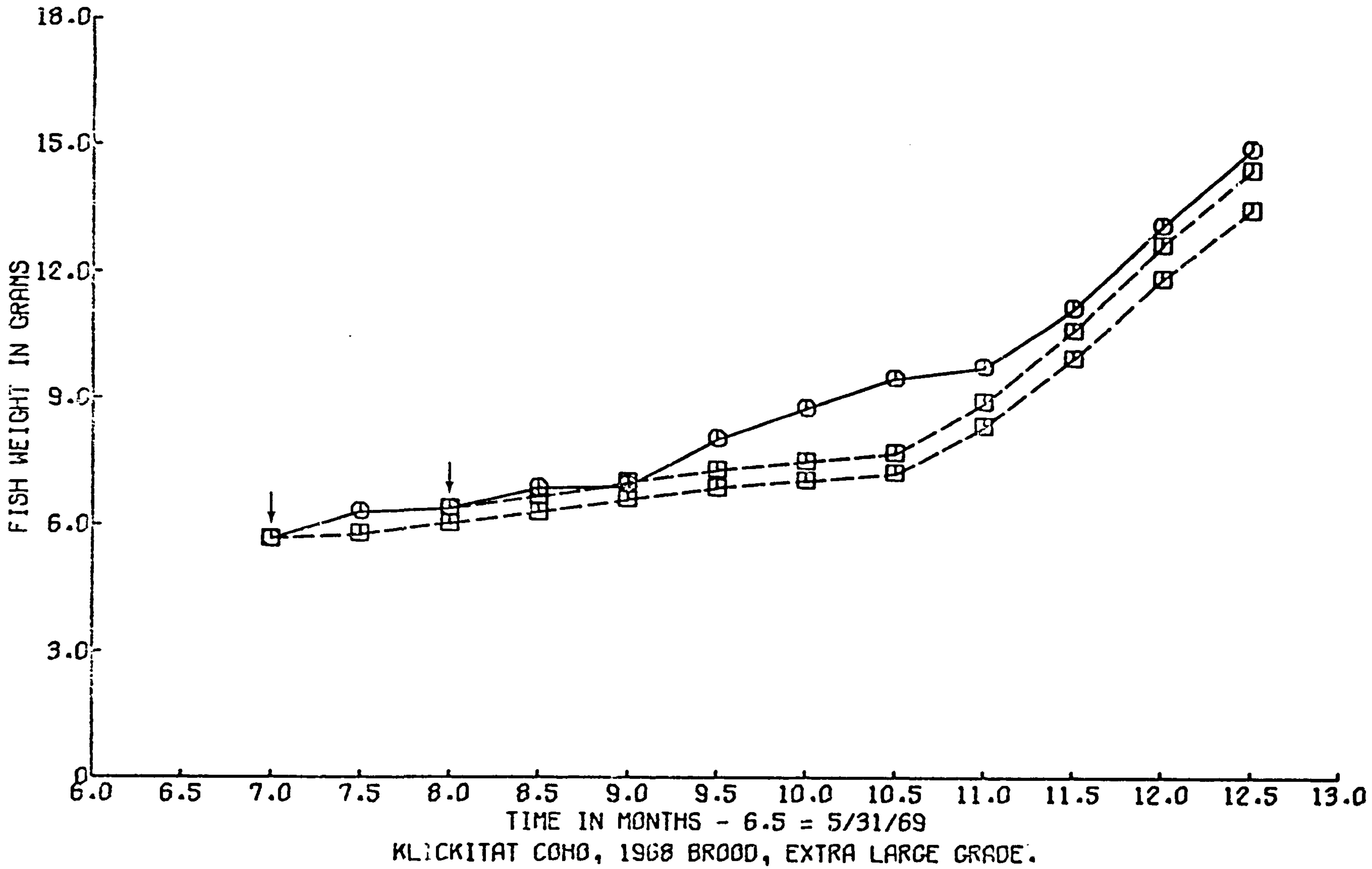


FIGURE 38. The observed (——) and the simulated (---) growth for the extra large grade lot of coho salmon from the 1968 brood reared at WDF Klickitat hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

the rearing ponds on 13 March 1969. The data were interrupted between 23 August and 20 September due to grading and mixing of the fish. Following 20 September the data were continuous until 24 January 1970 for only 78,000 fish. The simulation was started on 19 April and 20 September when the fish averaged 0.46 and 7.10 grams respectively. The results (Figure 39 and Table 8 of Appendix II) reproduce the observed weights quite well in the first half considering the initial weight was 0.46 grams. The predicted weights for the second half are slightly less than the observed but the final sizes are close. It should be noted that the average weekly temperatures peaked at 13.9°C (57°F) in the first week of month 7 and steadily decreased to 4.4°C (40°F) by the end of the simulation.

A second test lot was selected from the 1969 brood. The entire lot of 1.5 million was put in ponds on 17 March 1970. Only the records for one pond were processed for the simulation. The data were continuous from 13 June 1970 to 7 April 1971 the release date. The simulation was started on 13 June (month 7.0) when the fish averaged 2.34 grams and was stopped on 3 April 1971 (month 17.5) four days prior to the release. The results are shown in Figure 40 and Table 9 of Appendix II. The simulation greatly underestimated the growth of the fish initially. The predicted weights for months 8.0, 9.5, 10.0, and 10.5 were especially low for an unknown reason. The observed rations for the two weeks prior to these times were corresponding low. The fish were later marked and counted and this indicated that the inventory

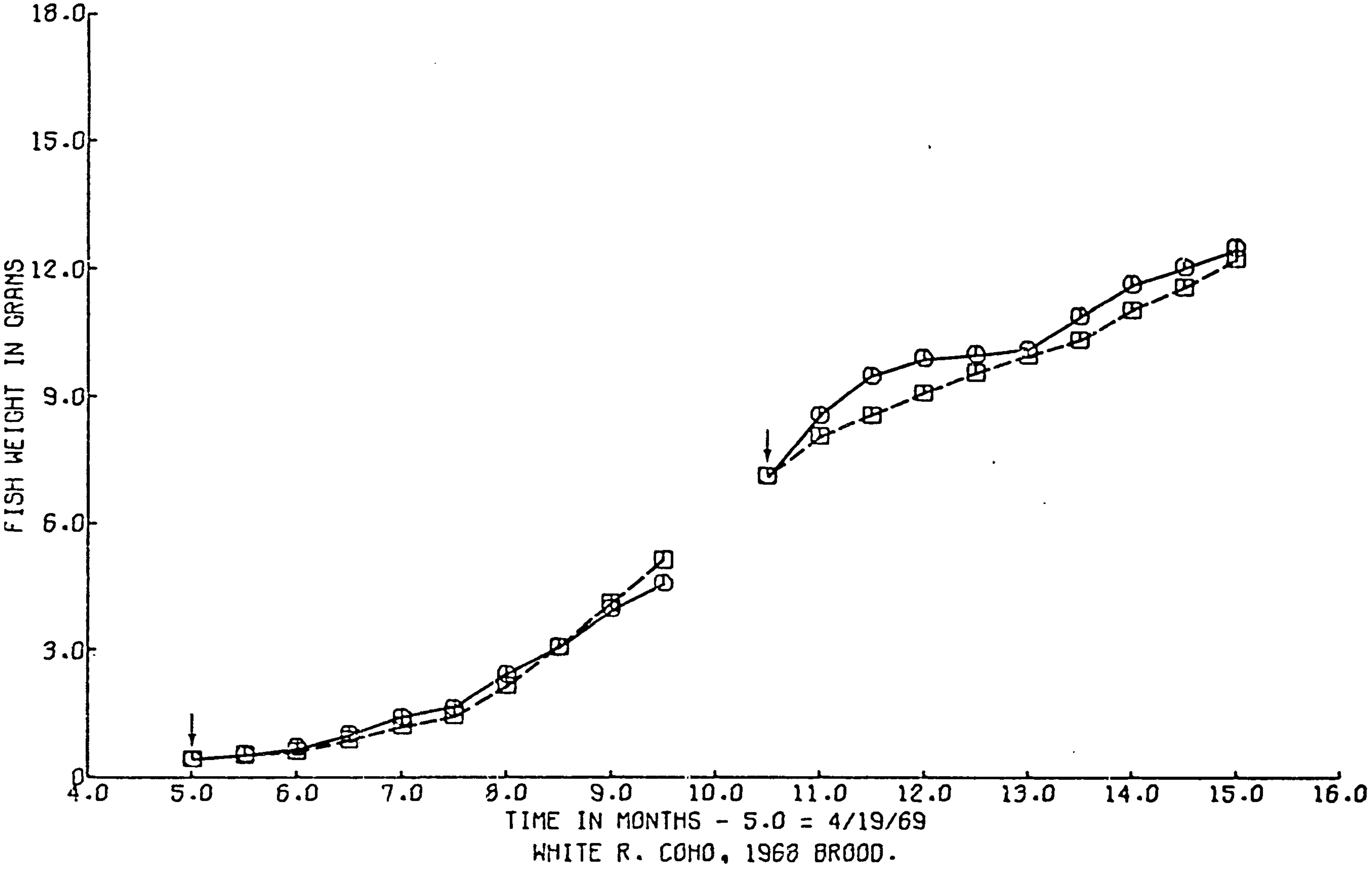


FIGURE 39. The observed (——) and the simulated (---) growth of the coho salmon from the 1968 White River brood reared at the WDF Minter Creek hatchery, the arrows indicate the start of simulation (1 month = 28 days).

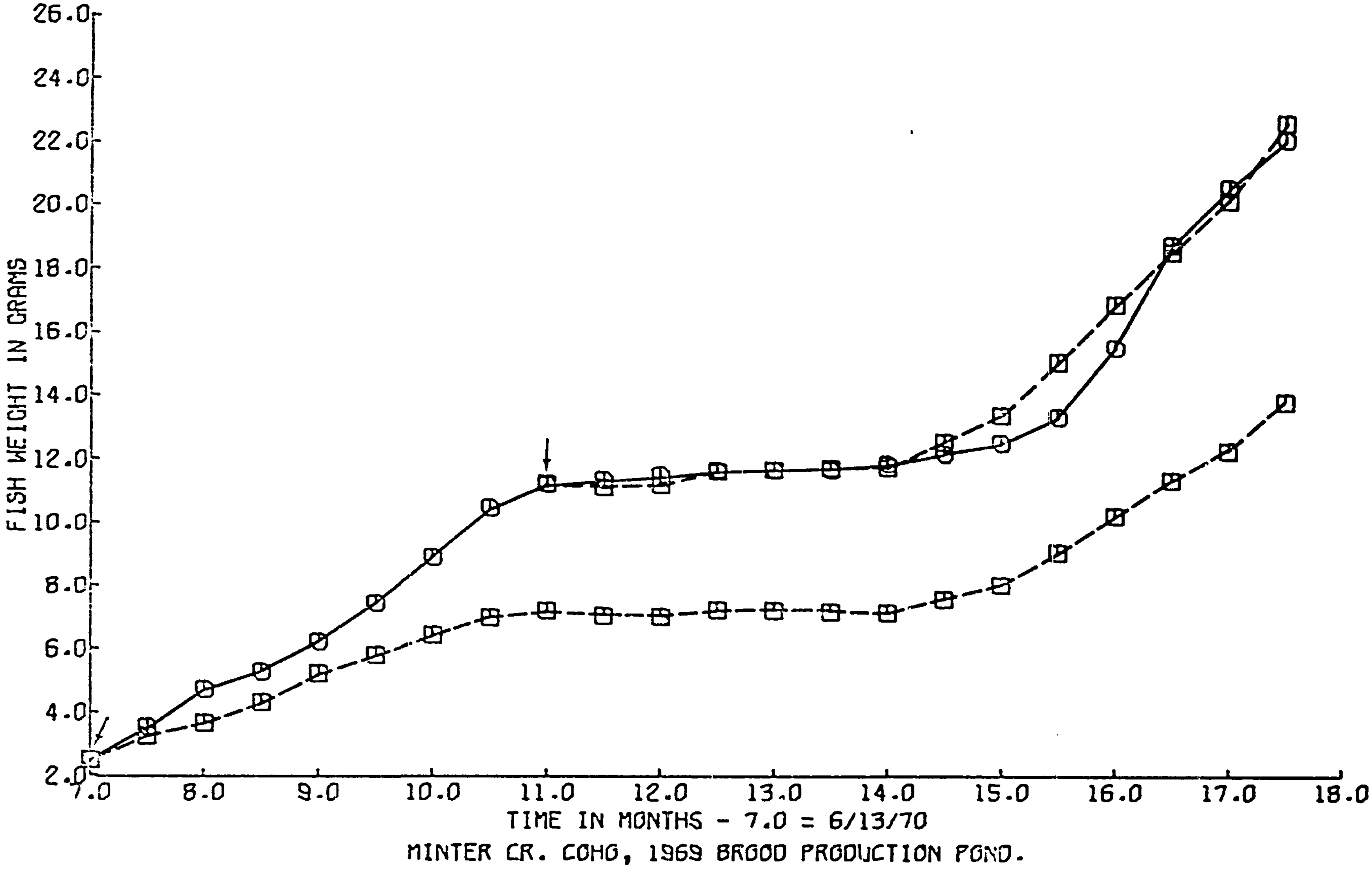


FIGURE 40. The observed (——) and the simulated (---) growth of the coho salmon from the 1969 brood reared at WDF Minter Creek hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

was accurate. The temperature averaged between 10 and 13°C (50 and 55°F) during this time. A restart of the simulation on 3 October (month 11), the first of three months of maintenance feeding, produced much better results. It should be noted that $\ell_3 = 0.0321$ is appropriate for this group of fish.

The ability of the model to predict the growth of coho salmon fed the Abernathy dry diet was examined. The needed data for two lots were available from the 1969 diet trials conducted at Minter Creek hatchery. The first lot was fed the moist Oregon diet and the other was fed the dry Abernathy diet. The 15,000 fish in each trial were selected from the same lot that was originally placed in the rearing ponds on 5 April 1969. The diet trials, though, started on 28 June and extended into February 1970. The simulations were started on the same date (month 7.5) but were stopped on 24 January (month 15.0) because the last weight sample was recorded on 30 January. The simulation results (see Figures 41 and 42 and Table 10 in Appendix II) agree with the observed up to month 11.0. Thereafter the predicted weights for both diet trials exceed the observed average weights. Specific two week periods that are the source of the discrepancies can be isolated for the lot fed the Abernathy diet. If the data are not in error, the simulation points out that the fish in the OPR lot did not respond in the normal manner between the months of 10.5 and 12.5. The causes of the discrepancies though are not known. The differences in the moisture content of the diets appear to have been properly accounted for. The simulation does not point out any differences between the diets. The simulation of the Oregon

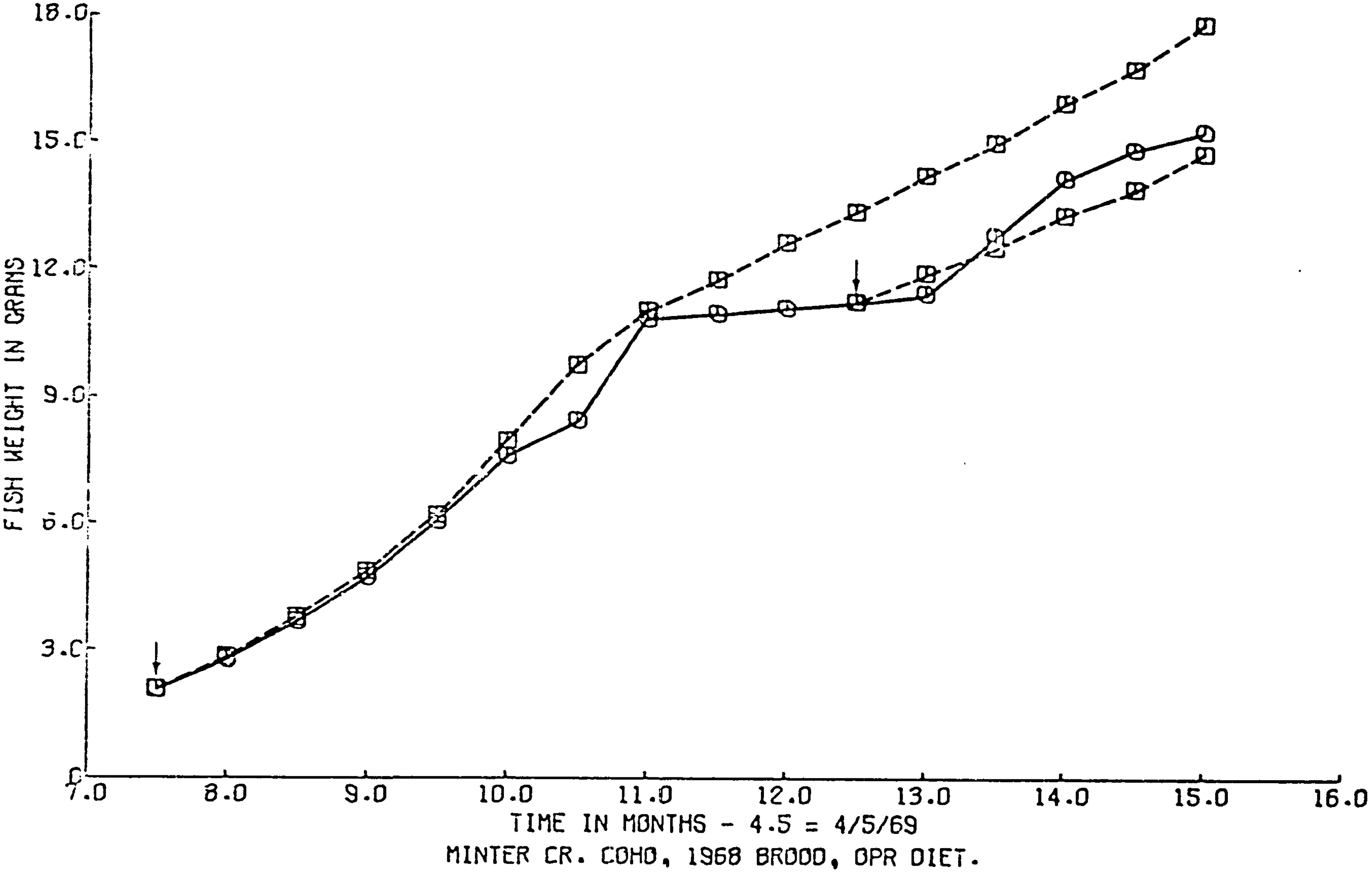


FIGURE 41. The observed (——) and the simulated (---) growth for a trial lot of coho salmon from the 1968 brood reared at the WDF Minter Creek hatchery and fed an Oregon diet, the arrows indicate the start and restart of the simulation (1 month = 28 days).

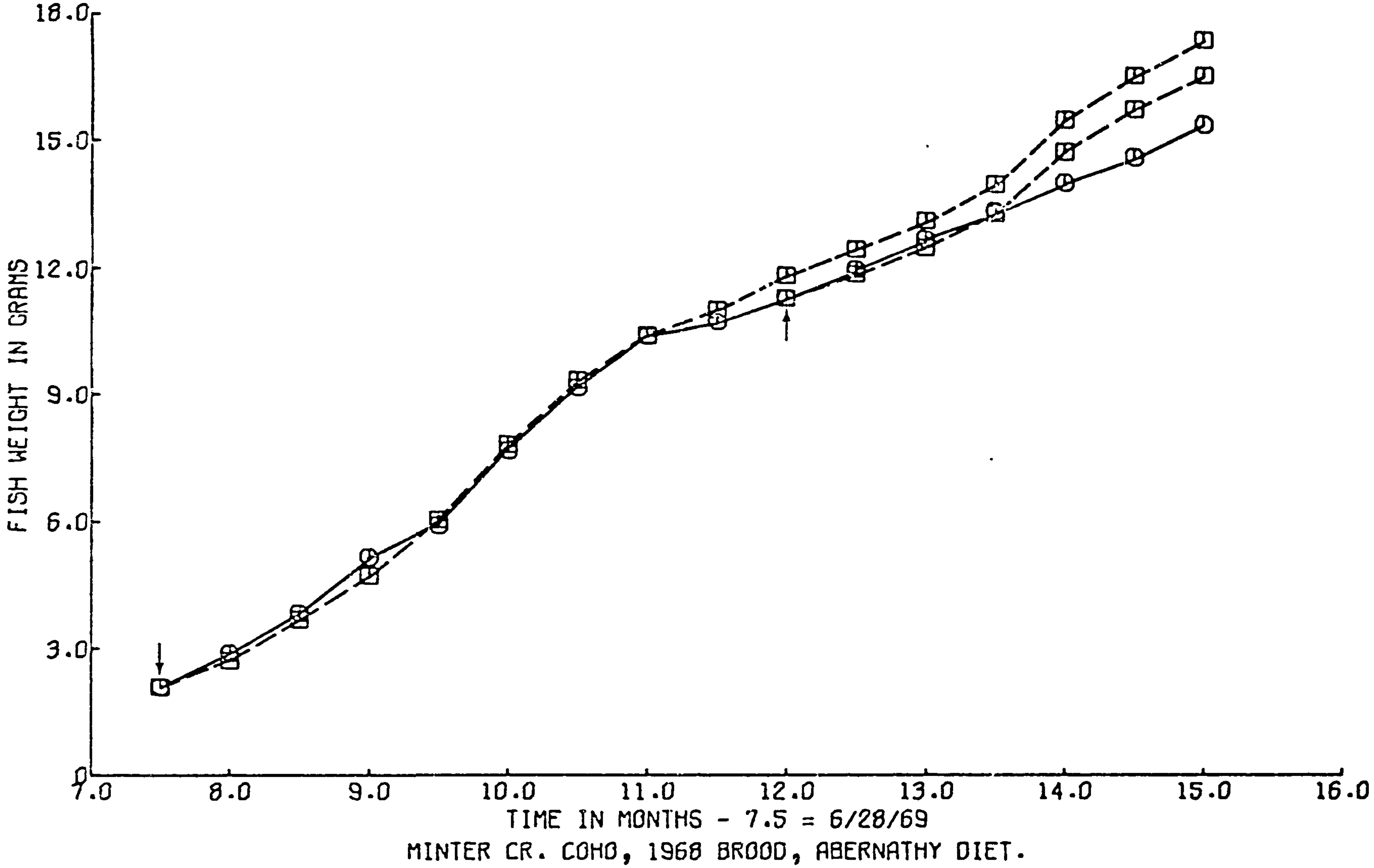


FIGURE 42 The observed (——) and the simulated (---) growth for a trial lot of coho salmon from the 1968 brood reared at the WDF Minter Creek hatchery and fed an Abernathy diet, the arrows indicate the start and restart of the simulation (1 month = 28 days).

diet lot is not totally independent of the equation coefficients since it was included in data set 2 of the coefficient optimization routine.

Oregon hatcheries

A goal of the Fish Commission of Oregon is to release coho smolts at an average size of 30 grams (Mr. D. Leith, personal communication). To achieve this, the daily rations are scheduled long in advance. Since this was not the case for the previously examined coho salmon, test data were retrieved from the records of three Oregon hatcheries. The data for two lots from the 1970 brood were available for the Sandy River hatchery. These lots were originally transferred as fry to the Sandy River hatchery from the Cascade and Klaskanine River hatcheries. The data for one pond from each lot were complete beginning on 1 August 1971. The fish were fed the OPR-2 diet until 6 November and the Abernathy dry diet thereafter. The fish were released at the end of April 1972.

Since the results of the simulations for the two lots were similar, only those for the 80,000 Klaskanine River fish reared in pond 10 are presented in Figure 43 and Table 11 of Appendix II. The simulation was started on 7 August (month 9.0) for the Oregon diet and 13 November (month 12.5) for the Abernathy diet. The simulation was terminated on 1 April 1972 three weeks before their release. It was necessary to restart the simulation twice. The first time was on 9.5. Between 9.0 and 9.5 the water temperature averaged 17.4°C (63.3°F), and the corresponding maintenance ration estimates were relatively high

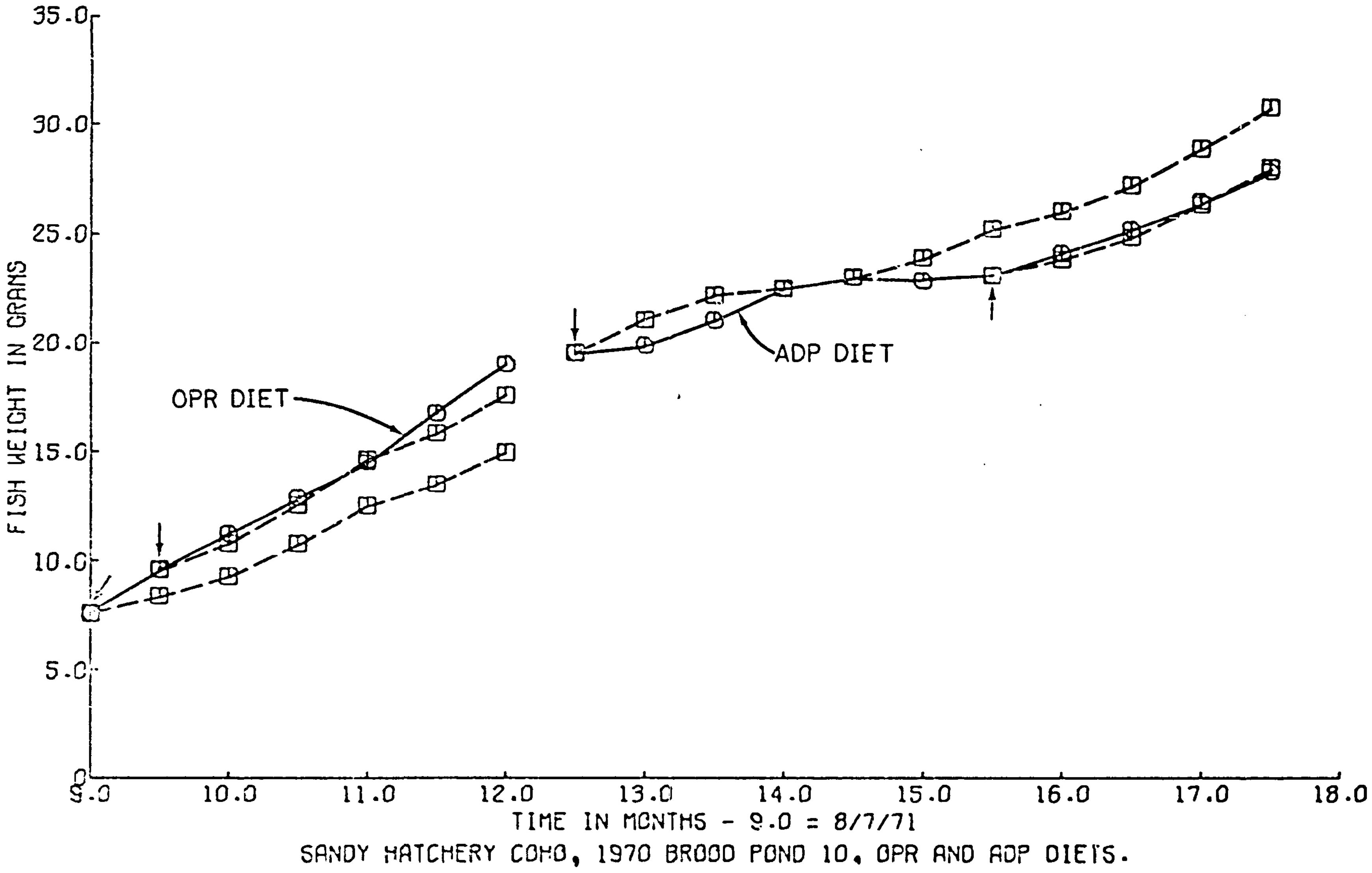


FIGURE 43. The observed (——) and simulated (---) growth of the coho salmon from the 1970 brood reared in pond 10 of the FCO Sandy River hatchery and fed the OPR diet and then the ADP diet, the shorter arrows indicate the start and restart of the simulation (1 month = 28 days).

Consequently, the simulation underestimated the observed growth rate for that time interval. The average temperatures rapidly dropped to 7°C (44.6°F) by the time of the diet switch. The simulator was restarted for a second time on 15.5. Up to this time the fish were fed the Abernathy diet at a level slightly above maintenance and the simulation did not reproduce the growth pattern. The predicted weights after the restart agreed with the observed.

The records for a number of lots from the 1969 and 1970 broods reared at the Cascade hatchery were screened. Of these, four were selected. The results of the simulations were similar for all four. Thus only the results for lot 2 and lot 1 from the 1969 and 1970 broods, respectively, will be presented. The data for lot 1 were included in data set 1 of the coefficient optimization routine. Both lots were placed in rearing ponds in early March and planted in the spring of the following year. The approximate numbers of fish in the lots were 275,000 for lot 2, 1969 and 525,000 for lot 1, 1970. The main diet was OPR-2. The simulation was started on 18 April 1970 (month 5.0) for lot 2 and 1 May 1971 for lot 1 when the fish averaged .805 and .85 grams respectively. It was stopped on 20 February 1971 (month 16.0) and 18 March 1972 (month 17.0) for the two lots respectively. Because the planting period was nearly a month long the simulations were terminated early. The simulations using the optimal coefficients produced fish almost twice the size of those recorded. The circumstances are similar to the simulations of the very small grade lot of the 1968 Klickitat coho salmon. The Oregon coho salmon are fed higher rations than Washington coho salmon in order to achieve a 30 gram smolt. On this basis FHMCT was reduced below 0.75 rather than reducing a_6 to a value below 0.0383 g/g/day. Satisfactory results were produced with FHMCT = 0.71. Also ℓ_3 was slightly reduced from 0.0321 to 0.0310 g/g/day to increase the simulated growth during periods of maintenance feeding. The predicted weights overestimated the observed sizes for lot 2 and underestimated those for lot 1 after three months. The results were improved by restarting the simulation at 8.0 and 9.5 for the two years respectively (see Figures 44 and 45, and Table 12 of Appendix II). The water temperatures increased from about 5 to 7°C (41 to 45°F) in May to temperatures above 15°C (59°F) in July. From then on the temperatures steadily dropped to near freezing values in January. The ponds froze over in the first week of February, 1972. Consequently, the fish were not fed. The simulation estimated that the maintenance ration was greater than the maximum and predicted a positive growth rate. Needless to say, this points out a weakness in the model for extremely low temperatures.

Identical results were obtained for coho salmon reared at Bonneville hatchery on the Columbia River one mile downstream from Cascade hatchery. Four lots from the 1969 and 1970 broods were selected and the simulation results were similar for all four. The simulation results for two of these are presented in Figure 46 and 47 and Table 13 of Appendix II. These are lot 2

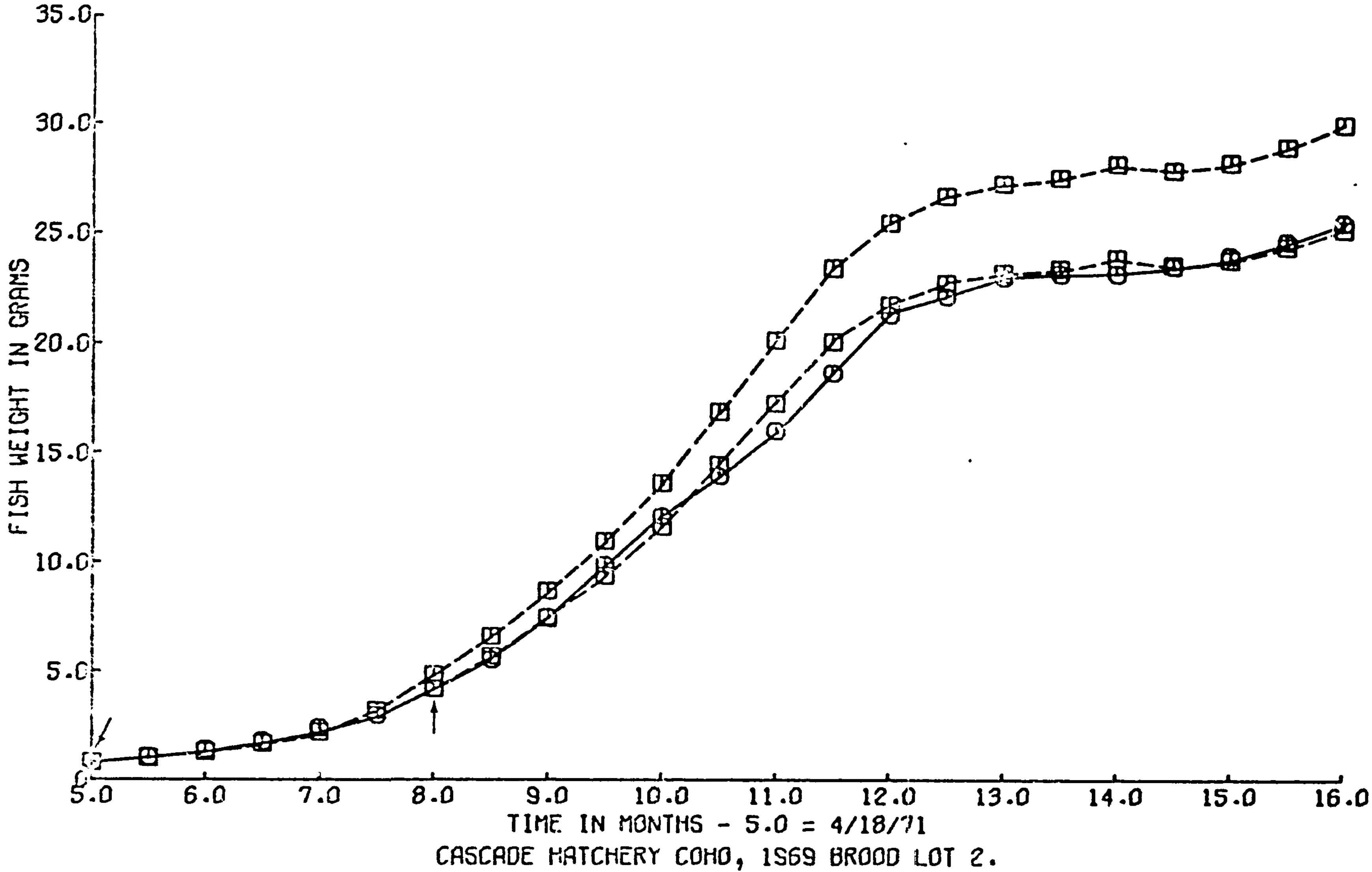


FIGURE 44. The observed (——) and the simulated (---) growth of the coho salmon in lot 2 of the 1969 brood reared at the FCO Cascade hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

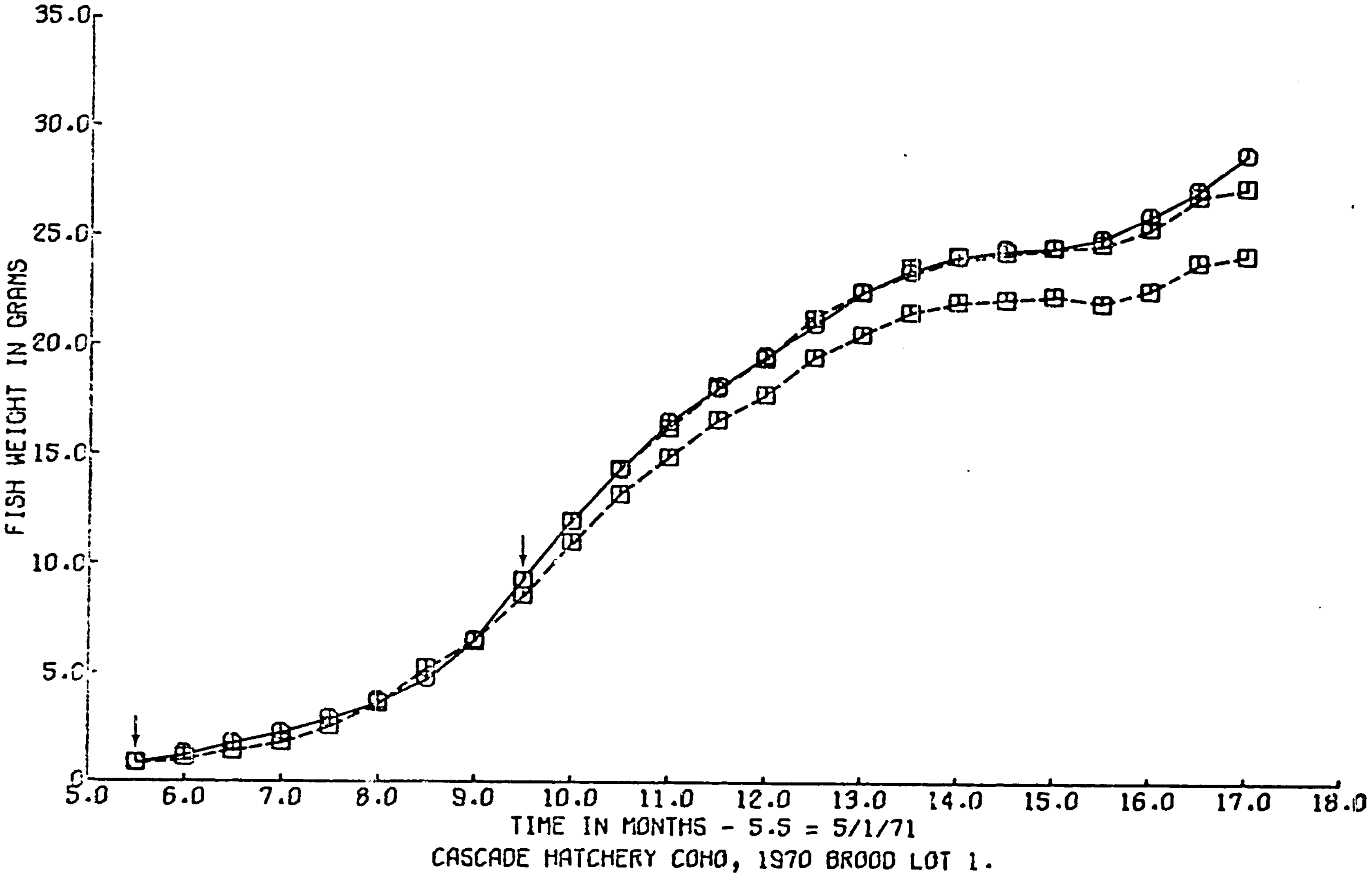


FIGURE 45 . The observed (——) and the simulated (---) growth of the coho salmon in lot 1 of the 1970 brood reared at the FCO Cascade hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

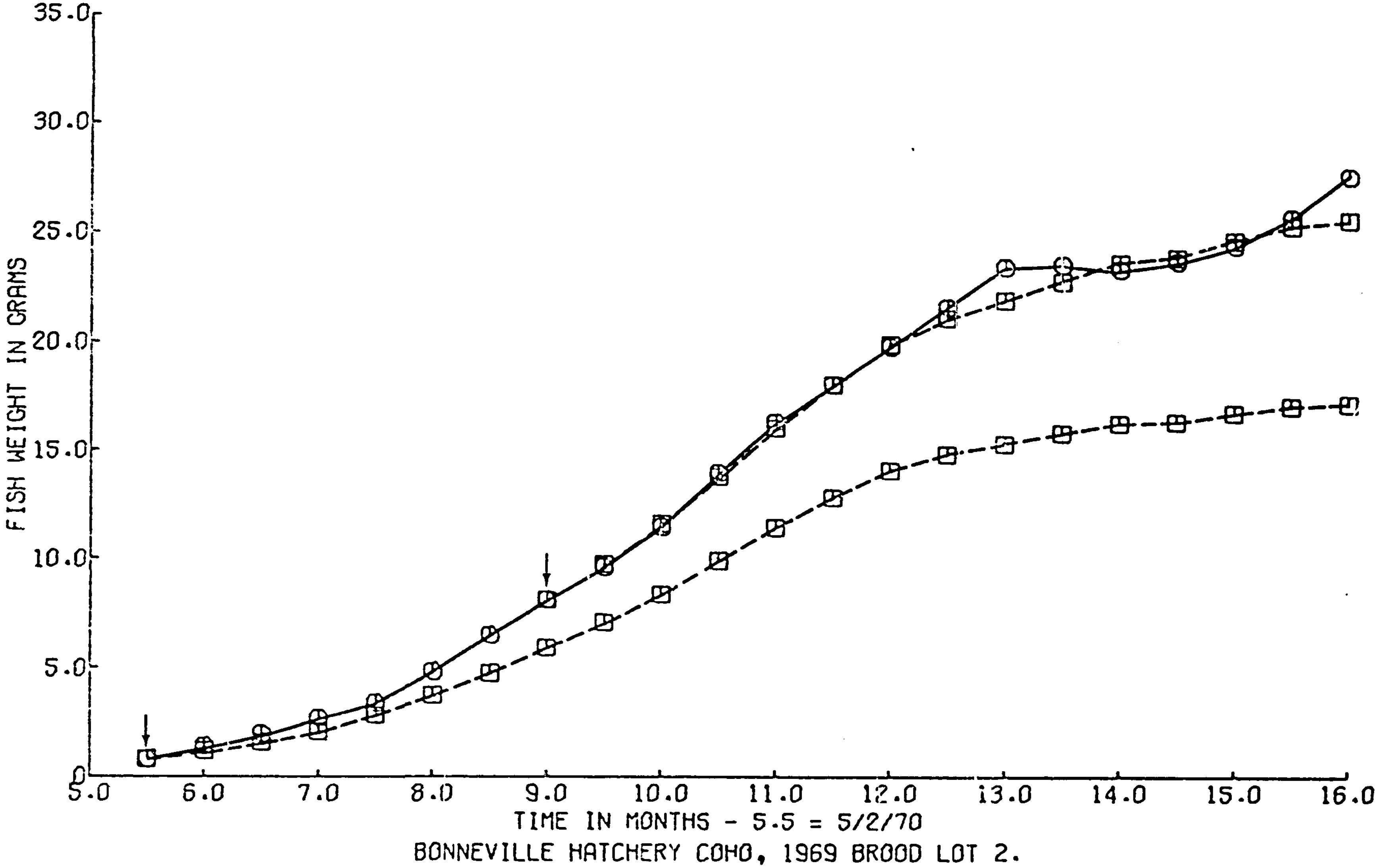


FIGURE 46. The observed (——) and the simulated (---) growth of the coho salmon in lot 2 of the 1969 brood reared at the FCO Bonneville hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

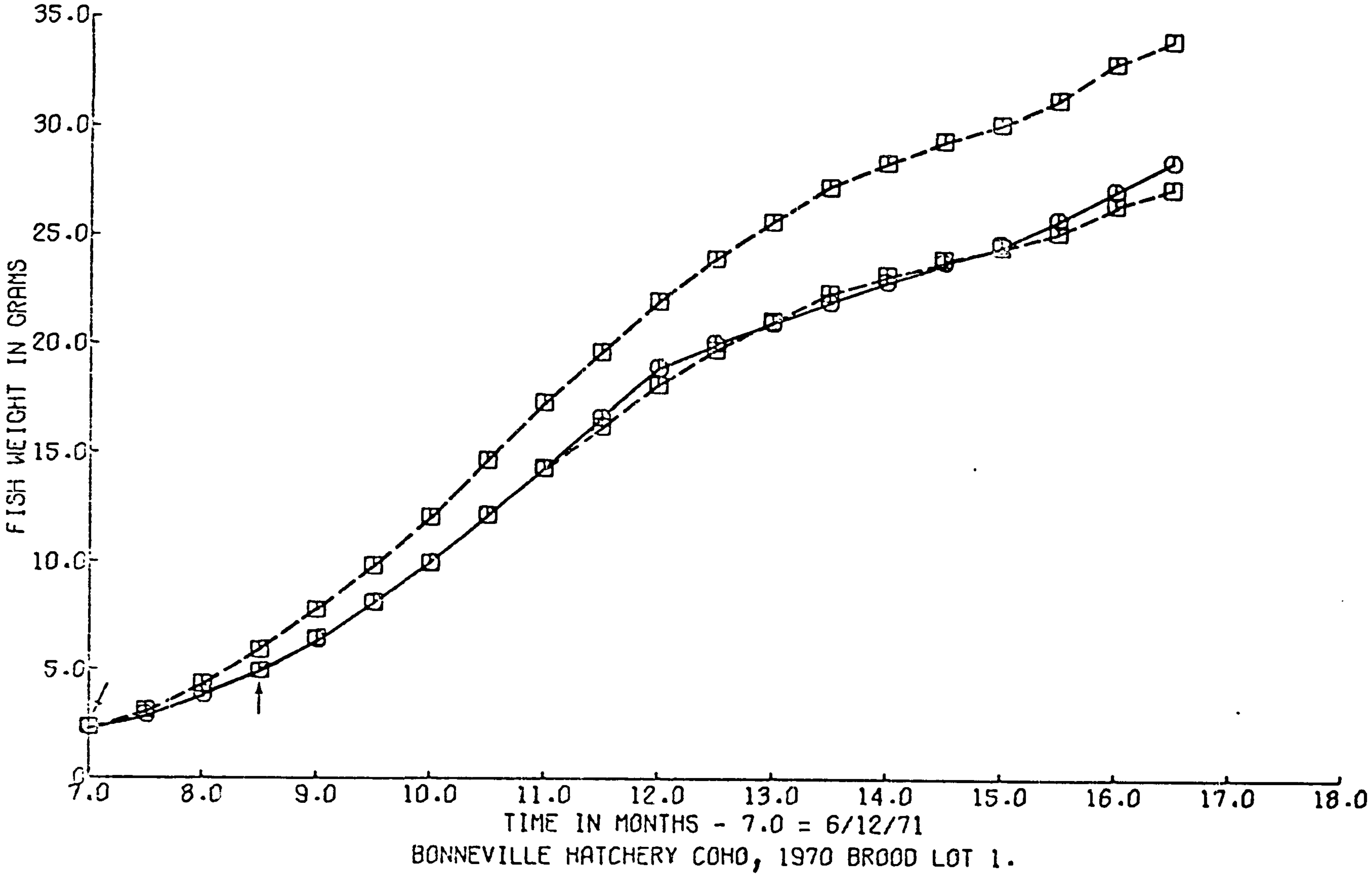


FIGURE 47. The observed (——) and the simulated (---) growth of the coho salmon in lot 1 of the 1970 brood reared at the FCO Bonneville hatchery, the arrows indicate the start and restart of the simulation (1 month = 28 days).

from the 1969 brood incubated at Bonneville and lot 1 from the 1970 brood incubated at Cascade hatchery. This lot was included in data set 2 of the coefficient optimization routine. The 1969 lot was placed in the rearing ponds in late March. The 1970 lot was transferred to Bonneville hatchery from Cascade hatchery on 3 June 1971. The simulation was run from 2 May 1970 (month 5.5) to 20 February 1971 (month 16.0) for the 1969 lot and from 12 June 1971 (month 7.0) to 26 February 1972 (month 16.5) for the 1970 lot. The data for each lot are from only one pond. The monitored pond for the 1969 lot was reduced from 540,000 to 180,000 fish in the middle of month 6 and again to 77,000 at the beginning of month 9.0. The monitored pond for the 1970 lot was reduced from 270,000 to 135,000 fish in the last week of month 7.0 and again to 72,000 one month later. The moisture content of the fish that provided the best results for the simulations was 71%. The predicted growth for the 1969 lot underestimated the observed growth up to the time of the last pond reduction. Those for the 1970 lot overestimated the observed growth up to the time of the last pond reduction. Also the value of ℓ_3 was increased from 0.0321 to 0.0360 g/g/day to lower the predicted growth rates during periods of low ration. The simulation was restarted for both lots just after the last pond reduction. The results simulated the observed growth quite well especially for the 1970 lot. Note the difference in the changes of ℓ_3 for the Bonneville and Cascade simulations. The Bonneville temperature cycle is similar to the temperatures at Cascade except the mid-summer high is less than 13°C (55°F).

The final data sets are two experimental lots of 1964 brood coho salmon reared at the Big Creek hatchery in Oregon. They were designed to test the survival of coho smolts released at 15 and 45 grams. The results of this experiment are reported by Johnson (1970). The rations fed to the lot released at the smaller size were about half the amount fed to the other lot. The diet was OPR-1. The two lots were selected from the same stock. There were 84,000 fish in the low ration lot and 60,000 in the high ration lot. The experiment started on 27 April 1965 and the fish were liberated on 18 March 1966. The initial size was 2.20 grams per fish. The low ration lot was included in the data set 2 of the coefficient optimization routine, and the other was in data set 1. The simulator was started on 27 April (month 5.0) and was terminated on 11 March 1966 (month 16.5). FHMCT was set at 0.75 for the low ration lot and 0.70 for the high ration lot. The value of ℓ_3 was reduced to 0.0240 g/g/day to stabilize the predicted growth rates during periods of maintenance feeding. The results of the simulation are shown in Figure 48 and Table 14 of Appendix II. The predicted weights for the low ration lot dropped below the observed weights in the first half of month 9. The simulation was corrected by restarting it at 9.5. The predicted weights for the high ration lot fell below the observed values early but never diverged from the real weights. The simulated weights of the high ration lot with FHMCT = 0.75 greatly exceeded the observed values as they did for the Cascade and Bonneville simulations. Since both

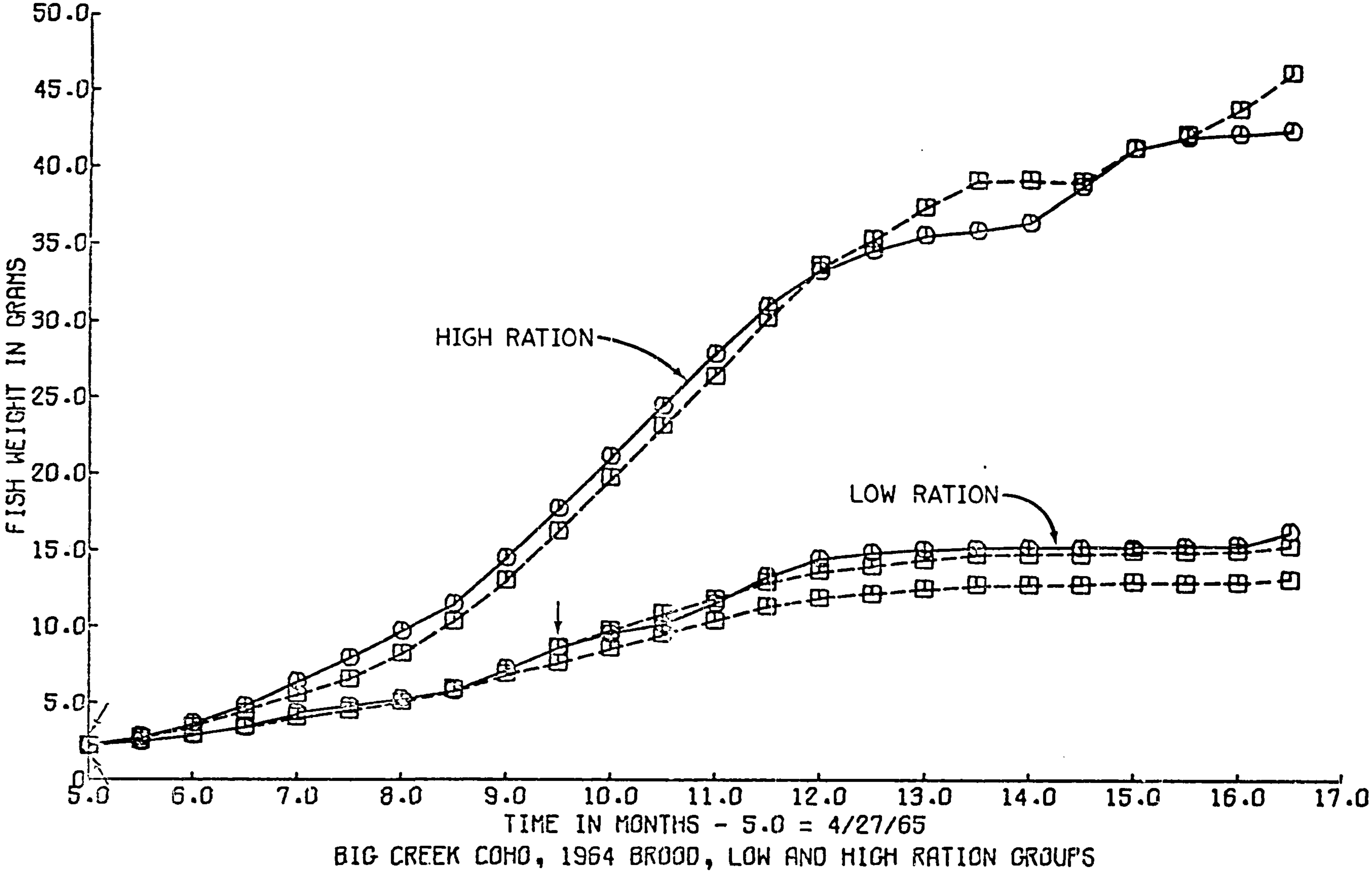


FIGURE 48. The observed (——) and the simulated (---) growth for the low and high ration lots of coho salmon from the 1964 brood reared at the FCO Big Creek hatchery, the shorter arrows indicate the start and restart of the simulation (1 month = 28 days).

lots originated from the same stock it does not make sense to reduce the value of a_6 for only the high ration. This would imply that the "scope for growth" was greater for the low ration lot. The simulation of these lots is important for two reasons; first, the high ration lot tests the model for coho salmon larger than normal, and second, they partially justify reducing FHMCT for fish with a history of high level rations.

A check on the hypothesis that the values of FHMCT were different for the two test lots of Big Creek coho salmon is now possible with the evidence recently made available by Mr. David Leith (FCO). In response to my inquiry, he provided the results of seven proximate analyses on hatchery reared coho salmon that included four from the Big Creek test lots. The moisture contents of the fish for the first two samples, taken on 17 November 1965 (month 12.5), were 71.4 and 75.1% for the high and low ration lots respectively. The values for the last two samples, taken on 16 March 1966 (month 16.5), were 71.5 and 76.3% respectively. The values and the magnitude of their difference do not agree with the hypothesized values. On the other hand, they partially confirm the hypothesis in that the moisture content for the high ration lot was considerably lower than that of the low ration lot. The increase in the moisture content of the low ration lot between the two sampling dates may be sampling error or it could be caused by the long period of maintenance feeding. Of the remaining three analyses, two were for the 1969 brood coho salmon reared at the Cascade hatchery and the other was for the 1970 brood coho salmon reared at the Big Creek hatchery. The two for the Cascade coho salmon should be representative of the fish from lot 2 shown in Figure 44. The moisture content for the Cascade coho salmon was 76.6% on 6 July 1970, when the fish were about 4.4 grams, and 73.8% on 27 March 1971 when they were 27.7 grams. The moisture content for the 1970 Big Creek fish was 74.2% prior to their March release. If the coho salmon in the low ration lot were representative of the fish reared by WDF, then one could conclude that a difference in the moisture content does exist between coho salmon reared under two feeding schedules in the manner hypothesized. On the other hand, the difference between the observed 71.5% and 75 to 76% is not as large as between 70% and 75% which provided the best results for the simulations.

In summary the simulations successfully reproduced the growth curve for 9 out of 15 chinook lots and 2 out of 15 coho lots without any modification to the coefficients or starting dates. By restarting at some intermediate date though the numbers of successful chinook and coho simulations were increased to 10 and 8 respectively. The greater number of restarts required for the coho simulations was probably the result of their longer duration. The longer the series of data the greater the chance for at least one error to occur in the data or for the moisture content of the fish to change significantly. In the case of the 1968 brood fall chinook lot fed the Oregon test diet lot at the Minter Creek hatchery it was necessary to increase a_6 from 0.0383 to 0.0460 g/g/day to achieve a satisfactory reproduction of the observed growth curve. Along this same line, the simulation of seven Oregon coho lots required either a decrease in FHMCT or a change in ℓ_3 or both. For six of the seven it was also necessary to restart the simulations around the end of the summer. On the other hand, satisfactory simulation results were never obtained for either the 1968 brood fall chinook lots from ponds 24 and 25 at the Klickitat hatchery or for the two lots of the 1969 brood fall chinook from the Green River hatchery.

SOURCES OF ERROR IN HATCHERY DATA

A number of possible sources of error in hatchery data have been suggested as probably causes of some of the discrepancies observed in many of the growth simulations. Errors in recording and transcribing the original hatchey data are hopefully minimal and insignificant. The likelihood of more serious errors is greater in the inventory records of the number and weight of fish on hand. Since it is too time consuming to count large numbers of individual fish, the initial number placed in the rearing ponds is estimated by the weight of the total group of fish placed in the pond multiplied by an estimate of the number of fish per pound. This estimate is subject to sampling and rounding errors. The numbers of mortalities are periodically subtracted from the records, keeping the number of fish on hand updated. Often when the fish are transferred or planted the inventory is corrected by reweighing the entire group and taking a new weight sample. In the process of calculating weekly averages of daily ration, the food consumption is divided by the number of fish on hand. If the recorded inventory is significantly in error, then the individual fish actually received a different amount of food than would be calculated. If the actual daily rations are underestimated then the growth simulator would predict weights that would be less than the observed. The opposite is true if the actual daily rations are overestimated. This type of error could have a relatively long term effect on the simulation. Unfortunately this error probably occurs frequently in hatchery records.

The periodic weight samples in units of numbers of fish per pound are subject to numerous errors. The most important are sampling and rounding errors. A considerable amount of work is required to obtain a representative sample of individuals from the population. Also the sample of fish, when it is weighed, should be void of any water that would add to the weight and reduce the number of fish per pound. These errors have a short term influence in the calculated daily ration if they are not common. If the initial weight used in the simulation is in error though, the effect on the simulation can be long term. If two groups of fish of two different sizes are combined the resulting population will be bimodal. A similar sort of thing may occur for a lot held in two or more ponds. In both cases the average weight of the fish will have a large variance. These cases should not be used as test data unless one is specifically studying the growth of biomodal populations. Often the average number of fish per pound is recorded to the nearest whole number. This rounding error becomes very significant for larger fish and may be the reason for fluctuating discrepancies in some of the simulations during the months prior to smoltification. Size selective removal of fish from a lot or pond can bias the observed growth rates. Cannibalism and "pinhead" mortality are examples where this can occur. This should be minimal in most cases.

In the early stage of development of the proposed growth model, it was assumed that the moisture content of fish flesh was 0.75. Brett, et.al. (1969) have demonstrated that the moisture content depends on the feeding history of the fish. The consequencies of changes in the moisture content have not yet been fully investigated. The Oregon coho studies using the present version of GROWTH indicate its long term influence in simulating growth.

Fluctuations in the moisture content of the food also can cause discrepancies to occur in the simulations. It was assumed that the Oregon pellets were 32% water and the Abernathy dry diets were 10% water. In reality these percentages may vary between pellet sizes, manufacturers, and mixing dates. The moisture content may also change during storage. The moisture content of the food is necessary to convert the daily ration from wet to dry weight values within the simulation. Fluctuations in the moisture of the food that result from changes in pellet sizes or diets could create an increasing discrepancy between the observed and predicted weights at some midpoint within the simulation.

Also in the early stages of development of the proposed growth model, it was assumed that the wastage of food was insignificant. This is probably a safe assumption in most cases but there are undoubtedly short periods of time when food is wasted. Some food is wasted intentionally when the fry are learning to feed. Additional food may be wasted if the diet is changed, or the size of the food particle is increased, or the fish are handled for some reason, or water temperatures suddenly change, or the water supply becomes turbid. The amount wasted may be considerably more if the fish are fed by automatic feeders. If food is wasted, then the calculated values of the daily rations will overestimate the actual values causing discrepancies in the simulation.

Finally, the weekly average of the daily minimum and maximum temperatures may differ from the actual temperature that the fish respond to on the average for a week, though this difference should be small. For most hatcheries the daily minimum and maximum temperatures are the only data available, leaving no other choice for simulation use. Aside from the problem of inaccurate thermometers, errors arising from this estimation procedure should be consistent throughout the simulation and should not cause short term discrepancies. Some confidence in the procedure for estimating the average temperatures is gained from the fact that the simulation predicted the growth of the salmon reared at the Klickitat hatchery and those reared at the hatcheries with highly variable temperatures about equally as well.

In future attempts to apply or verify the proposed growth model, all precautions must be taken to minimize these errors. New experiments must be designed with the idea of keeping accurate inventories, measuring daily food consumption precisely, using statistically sound sampling procedures in estimating fish weights or weighing the entire lot when possible, determining representative average water temperatures, and monitoring the moisture content of both the food and fish routinely.

PRELIMINARY SENSITIVITY ANALYSIS

A brief sensitivity analysis was undertaken to begin to understand the response of GROWTH to the various simulation options, errors and biases in the input data, and violations of initial assumptions. Three sets of hatchery data for which the simulator adequately reproduced the observed growth were selected for testing the sensitivity of the model. These are the late hatch lot of the 1970 brood fall chinook reared at the Green River hatchery (see Figure 28 and Table 3 of Appendix II), lot 2 of the 1969 brood Cascade Coho (see Figure 44 and Table 12 of Appendix II), and the large grade lot of the 1968 brood spring chinook reared at the Klickitat hatchery (see Figure 34 and Table 6 of Appendix II).

First the sensitivity of the model to various options for the length of the growth and printout intervals was investigated. As described earlier the growth can be incremented weekly or semimonthly and the results can be printed weekly, semimonthly or monthly. This yields five alternative combinations. Ration and temperature are constant within a printout interval even though growth may be incremented more than once. The combination of a 7 day growth interval with semimonthly printout was set as the standard option. The final predicted weights of the three test lots for the four other options were well within ±2% of the standard option. None of the simulated growth curves tended to diverge from the observed curves. The combination of the 7 day growth interval with weekly printout produced the smallest final weight for the three lots. The combination of the 7 day growth interval with monthly printout produced the largest final weight for the spring chinook and coho lots. Although the detail of weekly fluctuations was lost by increasing the length of both the intervals, accuracy of the predicted weight was not significantly sacrificed.

The sensitivity of the model to the value of initial weight was examined for the Green River fall chinook lot and the Cascade coho lot. In the case of the Cascade coho lot, the simulation was started on month 8.0 when the fish average 4.20 grams. Errors in the initial weight of ±1, 5, 10, and 20% were tried. In all cases the simulated growth curve diverged from the observed curve in absolute terms but maintained the same percentage error. Errors in the initial weight influence the entire length of simulated growth curve. If the rations are simulated then these errors only affect the first time interval.

Effects of bias in the average water temperatures was also examined for the three test lots. In the case of the Green River fall chinook salmon water temperatures increased almost linearly from 4.8 to 10.6°C (40.7 to 51°F) during the simulation and the rations were near the estimated maximum. When the temperature schedule is modified to increase linearly exactly, the simulation produced a growth curve almost identical to the observed as it did in Figure 28. A uniform increase in temperatures of either 1 or 3 Fahrenheit degrees increased the growth rates. If temperatures were to be increased further, then estimated maintenance rations would approach the observed rations causing a decrease in growth rate. A uniform drop in temperature of 1 Fahrenheit degree slightly reduced growth rates. For a -3° error in the temperatures, the observed rations exceeded the estimated maximum rations which greatly reduced the estimated growth rates. Except for the 3 degree drop, the final simulated weights did not vary more than ±0.2 gram from the observed.

The average temperatures for the spring chinook lot gradually decreased from 10.6 to 9.4°C (51 to 49°F) during the simulation illustrated in Figure 34. Alteration of the temperatures to a constant 10°C (50°F) or a linearly decreasing schedule of 10.6 to 9.4°C (51 to 49°F) did not greatly change the simulation results. The growth rates were depressed for those time intervals in which the modified temperatures were greater than the original. The effect of these lower rates though were cancelled by the increase in growth rates for those intervals in which the modified temperatures were less than the original. The increase in either temperature schedule of 1 and 2 Fahrenheit degrees decreased the predicted final weight 4 and 8 grams respectively. A similar decrease in the temperatures added 3.5 and 6 grams to the final predicted size. The effect of temperature was opposite that for the fall chinook because the rations were near the maintenance level.

The results of temperature modifications for the Cascade coho lot were similar to those for the spring chinook. In this case though the observed temperatures steadily decreased from 14.5°C (58.1°F) in the first week of computer month 8 to 4.4°C

(40°F) by the middle of month 13 and then remained relatively stable at 4.4°C to the end of the simulation. The rations were more than half of the estimated maximum ration during the first temperature phase and were slightly more than maintenance in the second. The simulation of the growth of this lot, using a temperature schedule that decreased linearly between 8.0 and 13.5 and remained constant at 4.4°C between 13.5 and 16.0, produced a growth curve almost identical to the one in Figure 44. A uniform change in this schedule of -2 or +2 Fahrenheit degrees caused the simulated growth curves to diverge and altered the final predicted weight by -2.7 and -3.3 grams respectively.

The predicted growth curves using the linear approximations to the observed temperatures were very similar to those of the original simulations for the three selected test lots. On the other hand, a uniform increase or decrease of 1 or 2 Fahrenheit degrees in the linearized temperature schedule was enough to produce distinct differences in the simulated growth curves, especially in the longer term Cascade coho and Klickitat spring chinook salmon. Except when rations were near the maximum in the case of the Green River fall chinook an increase in temperatures reduced the simulated growth rates and a decrease in temperatures increased the rates.

The sensitivity of GROWTH to the moisture content of the food and fish flesh has been demonstrated by a number of the simulations. In the present version of GROWTH, FDMCT and FHMCT are used only to convert the inputted rations from a wet weight to a dry weight basis and back. A one percentage point decrease in FDMCT increases the dry weight ration by about 1.5% for a moist diet and only about 0.5% for a dry diet. On the other hand, a one percentage point decrease in FHMCT reduces the dry ration value by about 4%. A check of the Green River chinook simulation showed that a two percentage point decrease in FDMCT raised the simulated growth curve and increased the predicted value of the final weight by an average of 0.9 grams or 3%. A one percentage point decrease in FHMCT decreased the final weight by 0.12 grams or 4% on the average. The simulated growth curve for FDMCT = 0.30 and FHMCT = 0.74 was almost identical to the original curve in Figure 28. The results of the check for the Cascade coho simulation were similar but more dramatic. For these fish a two percentage point decrease in FDMCT increased the final predicted weight by an average of 2.5 grams or 9%. A one percentage point decrease in FHMCT decreased the final weight by 3.0 grams or 11%. Also the simulated growth curve for FDMCT = 0.30 and FHMCT = 0.70 was almost identical to the one in Figure 44 where FDMCT = 0.32 and FHMCT = 0.71. The simulator is relatively insensitive to deviations in FDMCT especially if the food is a dry diet and the simulation is short in duration. On the other hand, the simulator in its present form is relatively sensitive to the value of FHMCT.

CONCLUDING COMMENTS

The proposed growth equation and the simulator predicted the growth of fish remarkably well in the numerous test situations considering the low precision of hatchery data and the high probability of inaccuracies therein. The functions that describe RMAINT, RMAX, and GMAX appear adequate for a wide range of sizes for the viable temperature range except near the extremes. The coefficients, particularly ℓ_3, a_6, and FHMCT, required only minor modification in some instances in order for the simulations to reproduce the observed growth curves. The sensitivity of the model to the moisture content of the fish temporarily limits its reliability in forecasting the growth of hatchery reared salmonids. The model, though, is the basis for such a forecast. The model also gives a common purpose to the numerous unrelated growth experiments conducted in years past.

The problem with the moisture content of the fish is twofold. First, the moisture content of hatchery reared salmonids is seldom measured. Consequently the moisture content of the fish will have to be estimated from the feeding records during the simulation. Second, the way in which the moisture content of the fish influences food consumption and food conversion must be determined. Then this information must be translated into adequate mathematical expressions so that the simulator properly handles the information.

Enough evidence is presented by Brett, et.al. (1969) in their Figure 9 to get a good start on estimating FHMCT from the feeding records. Their data can be described by the following exponential function

$$\hat{M}_{t+1} = M_{max} + (M_{maint} - M_{max}) \exp\left(-k\left(\frac{R_t-RMAINT}{RMAX-RMAINT}\right)\right) \quad (33)$$

where $\hat{M}_{t+1}$ is the estimated moisture content of the fish FHMCT at time t+1, M_{max} is the value observed for an extended period of maximum feeding. M_{maint} is the value observed for an extended period of maintenance feeding, R_t is the average ration fed during the interval t, t+1, and k is a constant. Initial trial estimates for M_{maint} and M_{max} from Bretts work are 0.79 and 0.72 respectively. A value of 3.0 for k would also be a good start. Hopefully the influence of size and temperature on the moisture content is accounted for by scaling the ration by RMAINT and RMAX. A time lag in the change of $\hat{M}_{t+1}$ can be simulated by using the exponential smoothing function, _i.e._,

$$\hat{\hat{M}}_{t+1} = C\hat{M}_{t+1} + (1-c)\hat{M}_t$$

where c is a constant of proportionality and has a value between 0 and 1. $\hat{M}_{t+1}$ is the value estimated by (33). If c has some intermediate value then the simulated moisture content depends partially on its value in previous time periods. If c = 1, then it equals the value estimated by (33). If c = 0, then it equals some constant initial value.

Presently the moisture content of the fish is used in GROWTH only to convert the daily rations to a dry weight basis. This may not be sufficient. RMAINT, RMAX, and GMAX are presently considered as constant for fish of a particular wet weight. This is implied in $f_2(W)$, $f_4(W)$, and $f_6(W)$ where W is in terms of wet weight. The alternative of scaling ℓ_3, ℓ_7, or a_6 by the dry weight of the fish should also be considered. The present use of FHMCT appears to be partially correct in that GROWTH predicted the difference in the moisture content of the coho salmon in the high and low ration lots from the Big Creek hatchery. Future simulation studies should give top priority to the modeling problems associated with a variable moisture content of the fish.

In light of these problems, the simulation results for the fall chinook salmon require further comment since these fish were fed rations near maximum throughout rearing. With this being the case, the moisture content of the fall chinook salmon may have been closer to 71 or 72% rather than 75% as assumed. A reduction in FHMCT reduces the dry weight value of the observed ration and consequently lowers the corresponding specific growth rate. To make up for the decrease in the estimated growth rates if FHMCT was decreased, a_6 would have to be increased to some value near 0.0420 g/g/day. If the new simulated growth curve fits the observed curve equally as well, then the new estimated food conversion factors based on wet weights will equal the previous ones. In this regard the old coefficients are adequate. On the other hand, simulations using the increased a_6 and the reduced FHMCT values could forecast greater growth for salmon fed rations near the maximum level since the values of GMAX and RMAX on a wet weight basis would be larger.

The second most important topic of future study should be to improve or correct the functions of RMAINT, RMAX, and GMAX for temperatures below 5°C (41°F) and above 15°C (59°F). As noted earlier the model may be inaccurate in these ranges. Since hatchery waters are often below 5°C in the winter months, it is important that the model be accurate in these temperatures. The weight function of these parameters should be checked out further for fish larger than 20 grams.

Once the moisture content problem is being handled properly and the functions of the three major parameters are confirmed for the temperature extremes and larger sizes then the model should be ready for one of its most important applications. This is forecasting the growth of hatchery reared coho and chinook salmon for a variety of feeding and temperature schedules. More specifically GROWTH could be used to find the most efficient ration schedule for a given temperature schedule that would grow coho or chinook salmon to a predetermined size by a certain date. If a system for heating and cooling the water supply were being considered for a hatchery, then the temperature schedule could also be manipulated to determine the best temperature settings.

In the future the model should be applied to other species, particularly rainbow and steelhead trout, sockeye salmon, catfish and other cultured spiny-rays. Culturing salmonids in seawater is becoming more common. In this presentation salinity was not considered, but it may have a significant influence on the growth of salmonids. Saltwater has the potential of reducing osmotic work and it may influence the moisture content of fish flesh. The model should be tried for saltwater rearing. Perhaps a more challenging application would be to predict the growth of fishes in natural environments. The main problem in this case would be estimating the average daily food consumption. Two possible approaches to solving this are to use an inverse expression of (33) to predict R_t from the moisture content of the fish as Brett, *et*. *al*. (1969) suggest. The other is to formulate a procedure to estimate the average food consumption per day from equation (15) which relates stomach contents to stomach size and rates of digestion.

As a final comment, the proposed model including the basic sine function and all its parts should not be considered as the best or final form. Future workers should try other equation forms that may be more appropriate. A future goal should be to replace the basic sine function with some other function with more biological meaning. Hopefully the proposed growth model will function as an organiser of thought and guide in future growth studies.

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APPENDIX I

FISHERIES ANALYSIS CENTER
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GROWTH

FORTRAN IV

Programmed by
Gary Dean Stauffer
1973

PROGRAM NO. FRS 741

GROWTH

IDENTIFICATION

FRS 741 - GROWTH
Gary Dean Stauffer - March 1973
College of Fisheries, University of Washington

PURPOSE

GROWTH is a CDC 6400 Fortran simulation model that predicts the growth of hatchery reared salmonids at weekly, semimonthly, or monthly intervals. The specific growth rates are determined from the average daily rations, average water temperatures, and the initial fish weight for each interval, A complete description of the specific growth rate function is given by Stauffer (1973). The model can be used to compare the predicted growth of the test fish with the observed. Also the model is capable of predicting the daily ration required to grow the fish to some predetermined size. GROWTH is an extensively abridged and modified version of the simulation model HATCH described by Rasch (1972).

PROGRAM DESCRIPTION

The program is set up to simulate either the growth or the daily ration of a single lot of fish at weekly, semimonthly, or monthly intervals. There are two clocks in GROWTH that indicate time. The "counter" tells the time by counting the iterations of time intervals during simulation. The "calendar" measures time in monthly units, 28 or 30.4 days long depending on user specification. The maximum duration of the simulation is 2 years. The main program calls a number of functions and subroutines that perform the actual calculations. Initially the program calls the subroutine TITLE. TITLE reads the first title card and prints out the corresponding heading. Next the subroutine INPT1 is called. INPT1 reads in five blocks of input data coded in KEYWRD free-field format (Gales and Sharpe, 1971). The first two blocks establish the contents of the printout and its format. The third block selects the option of simulating growth or ration and sets up the length of the two time intervals. The fourth set includes the hatchery data. In this set the simulation starting and ending dates, the number of fish, and average fish weight are inputted. The time tables of daily ration, average water temperatures and observed fish weights are set up. In the last block the values of the equation coefficients are inputted. On return from INPT1, the main program initializes the "counter" clock and calls the three subroutines INTLGR, PRNGRW, and HATCHR. These subroutines adjust the numbers of fish for natural mortalities, increment the biomass, select from the time tables the values of the ration R (g/g/day), temperature T (°F), and terminal observed weight WD (grams) for the current time interval. The rations are converted to a dry weight basis by

$$R_{dry} = R_{wet}\ (1-FDMCT)/(1-FHMCT)$$

where FDMCT is the moisture content of the food and FHMCT is the moisture content of the fish. HATCHR then calls the subroutine WTFN. WTFN increments growth of the fish or predicts the required ration. The fish are assumed to grow exponentially within the growth interval. The specific growth rate G is calculated by

$$G = GMAX \cdot \sin\left(\frac{\pi}{2}\left(\frac{R - RMAINT}{RMAX - RMAINT}\right)\right)$$

$$\text{where } GMAX = B1\left(A1 + A2 \cdot T + A3 \cdot T^{2} + A4 \cdot T^{3} + A5 \cdot T^{4}\right)\left(A6 \cdot W0^{-A7}\right)$$

$$RMAINT = B2\left(L1 \cdot 10^{L2 \cdot T}\right)\left(L3 \cdot W0^{-L4}\right)$$

$$RMAX = B3\left(-L5 + L6 \cdot ALOG(T)\right)\left(L7 \cdot W0^{-L8}\right)$$

and

B_i for i = 1,...,3 are the inputted BETAi adjustment coefficients
A_i for i = 1,...,7 are the inputted ALPH(i) growth coefficients
L_i for i = 1,...,8 are the inputted LAMBDA(i) growth coefficients.

If the user selects to predict the rations rather than simulate growth, then the value of R is adjusted by

$$R = MFCF\left((WD-W1)/W1\right)+R$$

where MFCF is the marginal food conversion factor inputted in the fifth data block and W1 is the predicted weight for the end of the current printout interval. R is continually adjusted until the following inequality is satisfied

$$\left|(WD-W1)/W1\right| \leq WERROR$$

where WERROR is the allowable error inputted in the third data block. The adjustment of R is also terminated when R has been asjusted WITER times where WITER is an integer also inputted in the third block.

Once the growth or ration is determined for the current interval, control is returned to HATCHR and the main program. Throughout these subroutines the values of various terms are stored in the output arrays. At this point the "counter" is incremented by 1 and INTLGR, PRNGRW, and HATCHR are recalled. This cycle continues until the counter exceeds the termination date. At the end of the simulation, the main program calls the subroutine YEARLY which prints out the requested data in tabular form. The values of the terms in each row of output apply to the beginning and the duration of that particular time interval.

If a job contains multiple runs then the main program restarts by recalling TITLE.

USAGE

Before using GROWTH it is recommended that the user put the binary version of the program on a tape file to eliminate the need of reading the program deck for every job. The user should also study the write up for KEYWRD subroutine (FRG 721). The input data for GROWTH has the following set up:

cards	keywords	description
Title card		one card with alphanumeric information in columns 1-80. The title card appears as the heading on the simulation output (manditory).

data Block #1

	Col. 1	
card 1	C‸INPUT PRINTER CONTROL	comment heading card.
2a	PRINT CARD‸	prints out the input data cards (default).
or b	SUPPR CARD‸	suppresses the printout of input data cards.
3	⟨blank card⟩	manditory data block separator.

data Block #2

	Col. 1	
card 1	C‸OUTPUT PRINTER CONTROL	comment heading card.

2a	EXPAN	expands output format for CDC line printer (default).
or b	SHRIN	skrinks output format for 80 column printer.
3	PRIMA	prints the primary hatchery statistics.
4	SECON	prints the secondary hatchery statistics.
5	TERTI	prints the tertiary hatchery statistics (for CDC line printer only).
6	PLOT‸	creates tape file of simulation results for SIMPLOT (Links, 1972).
7	PREVI	places plotting data on previous tape file.
8	⟨blank card⟩	manditory data block separator.

data Block #3

	Col. 1	
card 1	C‸SIMULATION OPTIONS	comment heading card.
2	CYCLE n	Length of printout interval, if n=1 printout interval = month, if n=2 printout interval = semimonth, if n=4 printout interval = week, only these three values are allowed.
3	WEEK‸ n	Length of growth interval in days/interval, if n=7.0 or 7.6 growth interval = week, if n=14.0 or 15.2 growth interval = semimonth.
4	AVERA TEMPE	If the printout interval is monthly, then the monthly value of water temperature is the average of the four weekly values. If this card is omitted then the value is the temperature at the middle of the month.
5	AVERA RATIO	The function of this card is the same as the previous, except the variable is daily ration.

6	WERROR <u>a</u>	WERROR = a, where a is some real number (default value = 0.0).
7	WITER <u>n</u>	WITER = n, where n is some integer (default value = 0).
8	⟨blank card⟩	manditory data block separator.

[note: The user may select the option of predicting ration by setting both WERROR and WITER equal to values greater than zero, recommended values are 0.01 and 5 respectively.]

<u>data Block #4</u>

<u>Col.</u>
1

card 1 C^TABLED INPUT comment heading card.

2 XQ^^^(1 *TO* 4) = ***(t_1,t_2,t_3,t_4)

3 YQ^^^(1 *TO* 4) = ***(0.,1.,1.,0.)

This table is the queue times for starting and stopping the simulation; time is in computer months; t_2 is the date of beginning of the first print-out interval, t_4 is the date of the end of the last interval, and t_1 and t_3 are some dates just prior to the t_2 and t_4 respectively.

4 XTEMP(1 *TO* 8) = ***($t_1,t_2,\ldots,t_8$)
XTEMP(m *TO* n) = ***($t_m,\ldots,t_n$)
YTEMP(1 *TO* 8) = ***($T_1,T_2,\ldots,T_8$)
YTEMP(m *TO* n) = ***($T_m,\ldots,T_n$)

This set of cards is the input temperature table where T_m is the water temperature in °F corresponding to time t_m in units of computer months.

5 XFDTB(1 *TO* 8) = ***($t_1,t_2,\ldots,t_8$)
XFDTB(m *TO* n) = ***($t_m,\ldots,t_n$)
YFDTB(1 *TO* 8) = ***($R_1,R_2,\ldots,R_8$)
YFDTB(m *TO* n) = ***($R_m,\ldots,R_n$)

This set of cards is the input ration table where R_m is the average daily ration in g/g/day for time t_m in computer months.

6	XDSRW(1 *TO* 8) = ***($t_1,t_2,\ldots,t_8$) XDSRW(m *TO* n) = ***($t_m,\ldots,t_n$) YDSRW(1 *TO* 8) = ***($W_1,W_2,\ldots,W_8$) YDSRW(m *TO* n) = ***($W_m,\ldots,W_n$)	This set of cards is the input predetermined desired weight table where W_1 is the wet weight of the fish in grams at time t_m in computer months.
7	INTLN n	This sets the initial number of fish equal to n.
8	INTLW w	This sets the initial weight of the fish equal to w grams.
9	⟨blank card⟩	manditory data block separator.

data Block #5

Col.
1

card 1	C∧EQUATION COEFFICIENTS	comment heading card.
2	LAMBD(1 *TO* 8) = ***($\ell_1,\ell_2,\ldots,\ell_8$)	The ℓ_i coefficients for the RMAINT and RMAX expressions.
3	ALPHA(1 *TO* 7) = ***($a_1,a_2,\ldots,a_7$)	The a_i coefficients for the GMAX expression.
4	BETA1 n BETA2 n BETA3 n BETA4 n	The beta coefficients are dummy variables that can be used to adjust GMAX, RMAINT, and RMAX values; recommend value of n is 1.0 in all four cases (manditory cards).
5	MFCF∧ n	The marginal food conversion factor is set equal to n; this is only manditory if user wants to predict rations; recommended value is 0.25.
6	FDMCT n	The number n is the percentage moisture content of the food divided by 100.
7	FHMCT n	The number n is the percentage moisture content of the fish divided by 100.

8	MORTA	n	This is the exponential mortality rate of fish reared in the hatchery on an annual rate.
9	<blank card>		manditory data block separator.

Repeat the title card and the five data blocks for additional runs within the same job. If the multiple runs are for the same test fish with only minor changes, then the repeated cards needs to include new title cards, KEYWRD comment cards, blank separator cards, and only the KEYWRD cards that are changed. KEYWRD cards that would be identical with the cards in the previous run do not need to be included in the subsequent run.

REFERENCES

Gales, L. E. and W. Sharpe. 1971MS. KEYWRD: A free-field input package. Univ. of Wash., Fisheries Analysis Center, Program No. FRG 721, 7p.

Links, D. 1972. SIMPLOT. Univ. of Wash., Computer Center Program Manual No. W00071.

Rasch, T. 1972. HATCH: a simulation model of a salmon hatchery. Master Thesis, Univ. of Wash., Seattle, 218p.

Stauffer, G. D. 1973. A growth model for salmonids reared in hatchery environments. Ph.D. Thesis, Univ. of Wash., Seattle, 213p.

SAMPLE JOB

The system cards for copying the binary version of GROWTH on to a tape file are:

```
 (job card) CM 55000
REQUEST.TAP,VRN=nnn.FILES=nn.OUT.HI.DI.
FORTRAN(MODE=G)
REWIND(LGO)
COPYBR(LGO.TAP)
REWIND(TAP)
7-8-9

     (GROWTH fortran source deck)

6-7-8-9
```

The following is an example set up for two runs with the binary version of GROWTH on tape. This job includes plotting weights from the two simulations on the same graph using SIMPLOT.

```
(job card) CM 53400
REQUEST.GROWTH.VRN=nnn.FILES=nn.IN,HI,DI.
NOREDUCE.
SETCORE.
MAP(OFF)
GROWTH.
ATTACH(SIMPLOT)
SIMPLOT.
7-8-9
FIRST SAMPLE RUN (1970 FALL CHINOOK GREEN RIVER LATE HATCH, OMP DIET)
C INPUT PRINTER CONTROL
PRINT INPUT FILE CARD
(blank card)
C OUTPUT CONTROL
PRINT TERTIARY GROWTH STATISTICS
PLOT  THE DATA FROM THE RESULTS OF THE SIMULATION
(blank card)
```

```
C SIMULATION OPTIONS
CYCLE  2 TIMES PER MONTH
WEEK EQUALS 7.0 DAYS
NITER = 0
 (blank card)
C TABLED INPUT
XO    ( 1 *TO* 4 ) = ***( 3.25,3.50,5.75,6.00 )
YO    ( 1 *TO* 4 ) = ***( 0.,1.,1.,0. )
XTEMP( 1 *TO* 8 ) = ***( 1.125,1.375,1.625,1.875,2.125,2.375,2.625,2.875 )
XTEMP( 9 *TO* 16 ) = ***( 3.125,3.375,3.625,3.875,4.125,4.375,4.625,4.875 )
XTEMP( 17 *TO* 24 ) = ***( 5.125,5.375,5.625,5.875,6.125,6.375,6.625,6.875 )
YTEMP( 9 *TO* 16 ) = ***( 41.,39.,40.5,41.,42.5,44.5,45.5,46. )
YTEMP( 17 *TO* 24 ) = ***( 46.,47.5,51.,51.,48.,52.,49.5,51. )
XFDTR( 1 *TO* 8 ) = ***( 1.125,1.375,1.625,1.875,2.125,2.375,2.625,2.875 )
XFDTR( 9 *TO* 16 ) = ***( 3.125,3.375,3.625,3.875,4.125,4.375,4.625,4.875 )
XFDTR( 17 *TO* 24 ) = ***( 5.125,5.375,5.625,5.875,6.125,6.375,6.625,6.875 )
YFDTR( 9 *TO* 16 ) = ***( .0026,.0232,.0215,.0284,.0371,.0381,.0414,.0369 )
YFDTR( 17 *TO* 24 ) = ***( .0375,.0324,.0366,.0379,.0383,.0383,.0383,.0383 )
XDSRW( 1 *TO* 8 ) = ***( 1.,1.25,1.5,1.75,2.,2.25,2.5,2.75 )
XDSRW( 9 *TO* 16 ) = ***( 3.,3.25,3.5,3.75,4.,4.25,4.5,4.75 )
XDSRW( 17 *TO* 24 ) = ***( 5.,5.25,5.5,5.75,6.,6.25,6.5,6.75 )
YDSRW( 9 *TO* 16 ) = ***( .463,.510,.575,.643,.735,.875,1.06,1.27 )
YDSRW( 17 *TO* 24 ) = ***( 1.50,1.82,2.08,2.64,3.12,3.60,0.,0. )
INTLN= 270000.
INTLW= .575
 (blank card)
C EQUATION COEFFICIENTS
LAMBD( 1 *TO* 8 ) = ***( .0397,.0280,.0321,.2165,8.82,2.51,.171,.3333 )
ALPH ( 1 *TO* 5 ) = ***( 15.949,1.3849,-.0460180,.00069698,-.000038991 )
ALPH ( 6 *TO* 7 ) = ***(  .0383,.3333 )
BETA1 = 1.
BETA2 = 1.
BETA3 = 1.
BETA4 = 1.
MFCF =  .25
FDMCT= .32
FHMCT = .75
MORTA= 0.0
 (blank card)
```

```
SECOND SAMPLE RUN (SAME FISH LOT BUT DIFFERENT ALPH(6) AND FHMCT VALUES)
C INPUT PRINTER CONTROL
 (blank card)
C OUTPUT CONTROL
USE PREVIOUS TAPE FOR PLOTTING
 (blank card)
C SIMULATION OPTIONS
 (blank card)
C TABLED INPUT
 (blank card)
C EQUATION COEFFICIENTS
ALPH ( 6 ) = .042
FHMCT= .72
(blank card)
7-8-9
VARIABLE LIST  TIME,PTN,DSPTN,RMAIN,RMAX,WT,DSRWT,TEMP
INPUT MEDIUM   TAPE14
INPUT FORMAT
MULTIPLOT      SYMBOL, TIME VERSUS WT/SYMBOL,TIME VERSUS DSRWT
BOTTOM LABELS  TIME IN MONTHS - 3.5 = 3/6/71
               GREEN RIVER FALL CHINOOK, 1970 BROOD LATE HATCH
SIDE LABELS    FISH WEIGHT IN GRAMS
STATISTICS     NONE
PLOT OPTIONS   HORIZONTAL= 8 INCH, 3.0 TO 6.0, DIVISIONS=  6, DIGITS= 1/
               VERTICAL= 5 INCH, 0.0 TO 6.0, DIVISIONS= 6, DIGITS= 1
FINISH
6-7-8-9
```

APPENDIX II

TABLE 1. The GROWTH input data and the corresponding simulated growth of the fall chinook salmon from the 1968 Spring Creek brood reared at WDF Klickitat hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
All 5 ponds combined					
3.00	49.0	.0311	.987	.0209	.987
3.25	49.0	.0289	1.23		
3.50	49.0	.0368	1.33	.0270	1.32
3.75	51.0	.0372	1.46		
4.00	49.0	.0341	1.85	.0239	1.93
4.25	49.0	.0327	2.25		
4.50	49.0	.0263	2.65	.0195	2.70
4.75	49.0	.0282	3.00		
5.00	50.0	.0272	3.35	.0190	3.55
5.25	49.0	.0257	3.73		
5.50			4.18		4.62
Pond 21 (or 22)					
3.50	49.0	.0373	1.34	.0254	1.34
3.75	51.0	.0325	1.68		
4.00	49.0	.0303	2.06	.0224	1.91
4.25	49.0	.0318	2.36		
4.50	49.0	.0240	2.90	.0178	2.62
4.75	49.0	.0263	3.30		
5.00	50.0	.0262	3.58	.0189	3.35
5.25	49.0	.0266	3.85		
5.50			4.15		4.37
Pond 23					
3.50	49.0	.0421	1.09	.0311	1.09
3.75	51.0	.0435	1.18		
4.00	49.0	.0368	1.58	.0254	1.68
4.25	49.0	.0340	1.95		
4.50	49.0	.0251	2.45	.0192	2.40
4.75	49.0	.0287	2.65		
5.00	50.0	.0267	3.10	.0188	3.14
5.25	49.0	.0259	3.54		
5.50			4.12		4.09

TABLE 1. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Pond 24					
3.50	49.0	.0350	1.40	.0248	1.40
3.75	51.0	.0332	1.62		
4.00	49.0	.0341	1.85	.0239	1.98
4.25	49.0	.0326	2.25		
4.50	49.0	.0266	2.53	.0197	2.77
4.75	49.0	.0285	2.93		
5.00	50.0	.0280	3.35	.0183	3.65
5.25	49.0	.0233	3.95		
5.50			4.23		4.72
Pond 25					
3.50	49.0	.0359	1.40	.0261	1.40
3.75	51.0	.0357	1.62		
4.00	49.0	.0370	1.85	.0253	2.02
4.25	49.0	.0350	2.25		
4.50	49.0	.0316	2.53	.0219	2.88
4.75	49.0	.0304	2.93		
5.00	50.0	.0272	3.35	.0179	3.91
5.25	49.0	.0229	3.95		
5.50			4.23		5.02

TABLE 2. The GROWTH input data and the corresponding simulated growth for two lots of fall chinook salmon from the 1969 brood reared at WDF Green River hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Early Hatch					
3.00	42.5	.0291	.685	.0210	.685
3.25	41.5	.0316	.807		
3.50	43.0	.0316	.950	.0215	.919
3.75	44.5	.0304	1.15		
4.00	44.5	.0341	1.28	.0231	1.24
4.25	45.5	.0348	1.43		
4.50	46.0	.0339	1.70	.0242	1.72
4.75	46.5	.0523	2.15		
5.00	47.0	.0394	2.70	.0224	2.41
5.25	46.5	.0331	3.35		
5.50	50.0	.0356	3.90	.0181	3.30
5.75	49.0	.0152	4.50		
6.00			4.95		4.25
Late Hatch					
3.50	43.0	.0274	.600	.0203	.600
3.75	44.5	.0299	.715		
4.00	44.5	.0370	.860	.0246	.797
4.25	45.5	.0344	1.00		
4.50	46.0	.0451	1.26	.0268	1.12
4.75	46.5	.0509	1.55		
5.00	47.0	.0395	2.23	.0250	1.64
5.25	46.5	.0375	2.83		
5.50	50.0	.0385	3.50	.0249	2.32
5.75	49.0	.0393	4.30		
6.00			4.70		3.29

TABLE 3. The GROWTH input data and simulated growth for three lots of fall chinook salmon from the 1970 brood reared at WDF Green River hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Early hatch, ADP diet trial					
3.50	40.5	.0210	.700	.0192	.700
3.75	41.0	.0213	.805		
4.00	42.5	.0263	.940	.0229	.916
4.25	44.5	.0257	1.06		
4.50	45.5	.0265	1.28	.0231	1.26
4.75	46.0	.0238	1.58		
5.00	46.0	.0263	1.98	.0221	1.74
5.25	47.5	.0215	2.30		
5.50	51.0	.0231	2.65	.0238	2.37
5.75	51.0	.0261	3.12		
6.00			3.55		3.31
Early hatch, OPR diet trial					
3.50	40.5	.0335	.738	.0199	.738
3.75	41.0	.0334	.845		
4.00	42.5	.0382	.955	.0235	.975
4.25	44.5	.0401	1.09		
4.50	45.5	.0393	1.38	.0246	1.35
4.75	46.0	.0363	1.70		
5.00	46.0	.0362	2.05	.0232	1.91
5.25	47.5	.0331	2.40		
5.50	51.0	.0337	2.77	.0257	2.64
5.75	51.0	.0378	3.30		
6.00			4.10		3.79
Late hatch, OPR diet trial					
3.50	40.5	.0215	.575	.0179	.575
3.75	41.0	.0284	.643		
4.00	42.5	.0371	.735	.0248	.739
4.25	44.5	.0381	.875		
4.50	45.5	.0414	1.06	.0262	1.04
4.75	46.0	.0369	1.27		
5.00	46.0	.0375	1.50	.0241	1.51
5.25	47.5	.0324	1.82		
5.50	51.0	.0366	2.08	.0270	2.11
5.75	51.0	.0379	2.64		
6.00			3.12		3.08

TABLE 4. The GROWTH input data and the corresponding simulated growth for two lots of fall chinook salmon from the 1968 brood reared at WDF Minter Creek hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
OPR - herring diet trial with $a_6 = .0383$					
5.00	49.5	.0328	.780	.0271	.780
5.25	49.5	.0420	.975		
5.50	52.0	.0410	1.25	.0304	1.14
5.75	51.0	.0412	1.60		
6.00	53.5	.0491	2.10	.0343	1.75
6.25	51.5	.0507	2.85		
6.50	55.5	.0567	3.80	.0347	2.82
6.75	56.0	.0516	4.75		
7.00			6.00		4.59
OPR - herring diet trial with $a_6 = .0460$					
5.00	49.5	.0328	.780	.0326	.780
5.25	49.5	.0420	.975		
5.50	52.0	.0410	1.25	.0365	1.23
5.75	51.0	.0412	1.60		
6.00	53.5	.0491	2.10	.0395	2.05
6.25	51.5	.0507	2.85		
6.50	55.5	.0567	3.80	.0384	3.57
6.75	56.0	.0516	4.75		
7.00			6.00		6.11
ADP - diet trial with $a_6 = .0383$					
5.50	52.0	.0365	1.08	.0328	1.08
5.75	51.0	.0306	1.35		
6.00	53.5	.0379	1.68	.0346	1.71
6.25	51.5	.0385	2.18		
6.50	55.5	.0384	2.80	.0346	2.78
6.75	56.0	.0396	3.65		
7.00			4.45		4.51

TABLE 5. The GROWTH input data and the corresponding simulated growth of the fall chinook salmon from the 1968 Finch Creek brood reared at WDF Minter Creek hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
7.00	57.0	.0420	1.05	.0328	1.05
7.25	53.5	.0466	1.40		
7.50	53.0	.0491	1.85	.0322	1.66
7.75	53.0	.0383	2.38		
8.00	53.5	.0567	2.93	.0322	2.61
8.25	53.5	.0404	3.65		
8.50	53.0	.0438	4.35	.0260	4.09
8.75	52.5	.0306	5.20		
9.00	52.5	.0371	6.30	.0234	5.90
9.25	52.5	.0319	8.40		
9.50	51.0	.0341	10.20	.0183*	8.18
9.75	51.0	.0222	11.15		
10.00	51.0	.0138	13.15	.0078	13.2 *
10.25	50.5	.0127	13.85		
10.50	51.5	.0128	14.55	.0096	14.7
10.75	50.5	.0167	15.25		
11.00	47.5	.0163	16.20	.0089	16.8
11.25	45.0	.0099	17.40		
11.50	46.0	.0145	18.60	.0099	19.0
11.75	46.5	.0146	19.75		
12.00			20.75		21.8

* predicted values for the simulation restart at 9.50.

TABLE 6. The GROWTH input data and the corresponding simulated growth of the spring chinook salmon from the 1968 brood graded into three size groups and reared at WDF Klickitat hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Small grade					
7.00	50.5	.0202	2.60	.0113	2.60
7.25	51.0	.0185	2.85		
7.50	51.0	.0206	3.12	.0120	3.04
7.75	51.0	.0190	3.40		
8.00	51.0	.0156	3.70	.0051	3.60
8.25	51.0	.0116	4.00		
8.50	50.0	.0149	4.26	.0057	3.87
8.75	50.5	.0121	4.38		
9.00	51.0	.0179	4.55	.0100	4.19
9.25	50.5	.0165	4.95		
9.50	50.5	.0175	5.32	.0102	4.82
9.75	50.5	.0165	5.65		
10.00	51.0	.0176	6.00	.0107	5.55
10.25	50.5	.0169	6.25		
10.50	50.0	.0217	6.55	.0145	6.45
10.75	49.0	.0194	7.30		
11.00	49.5	.0256	8.10	.0168	7.89
11.25	49.0	.0229	9.05		
11.50	49.0	.0176	9.95	.0118	9.98
11.75	50.0	.0166	10.55		
12.00	49.0	.0171	11.20	.0123	11.8
12.25	49.0	.0181	12.10		
12.50	48.5	.0168	13.00	.0104	14.0
12.75	48.5	.0136	13.85		
13.00	48.5	.0148	14.65	.0082	16.2
13.25	48.5	.0106	15.40		
13.50	49.0	.0107	16.15	.0094	18.1
13.75	49.5	.0172	17.00		
14.00			17.65		20.7

TABLE 6. continued

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Medium grade					
7.00	50.5	.0117	3.45	.0219	3.45
7.25	51.0	.0107	3.77		
7.50	51.0	.0149	4.05	.0089	3.56
7.75	51.0	.0186	4.27		
8.00	51.0	.0158	4.48	.0065	4.03
8.25	51.0	.0131	4.70		
8.50	50.0	.0149	4.88	.0059	4.41
8.75	50.5	.0119	4.95		
9.00	51.0	.0174	5.10	.0095	4.79
9.25	50.5	.0156	5.75		
9.50	50.5	.0177	6.37	.0107	5.47
9.75	50.5	.0168	6.70		
10.00	51.0	.0175	7.15	.0100	6.35
10.25	50.5	.0153	8.15		
10.50	50.0	.0178	9.15	.0117	7.31
10.75	49.0	.0170	9.60		
11.00	49.5	.0202	10.03	.0141	8.61
11.25	49.0	.0199	10.20		
11.50	49.0	.0202	10.50	.0136	10.5
11.75	50.0	.0185	11.45		
12.00	49.0	.0137	12.40	.0099	12.7
12.25	49.0	.0159	13.35		
12.50	48.5	.0148	14.35	.0087	14.6
12.75	48.5	.0119	15.20		
13.00	48.5	.0135	15.62	.0073	16.5
13.25	48.5	.0102	16.05		
13.50	49.0	.0105	16.50	.0083	18.3
13.75	49.5	.0152	17.00		
14.00	49.0	.0111	17.65	.0084	20.5
14.25	49.0	.0143	18.25		
14.50			19.10		23.1

TABLE 6. continued

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Large grade					
7.50	51.0	.0133	5.38	.0092	5.38
7.75	51.0	.0190	5.74		
8.00	51.0	.0128	6.10	.0021	6.12
8.25	51.0	.0075	6.47		
8.50	50.0	.0086	6.80	-.0005	6.31
8.75	50.5	.0066	7.00		
9.00	51.0	.0078	7.20	-.0008	6.26
9.25	50.5	.0076	7.40		
9.50	50.5	.0078	7.57	-.0005	6.19
9.75	50.5	.0078	7.67		
10.00	51.0	.0085	7.77	.0059	6.15
10.25	50.5	.0175	7.87		
10.50	50.0	.0177	8.00	.0117	6.68
10.75	49.0	.0173	8.22		
11.00	49.5	.0195	8.55	.0128	7.86
11.25	49.0	.0175	9.55		
11.50	49.0	.0194	10.50	.0130	9.41
11.75	50.0	.0178	11.45		
12.00	49.0	.0131	12.40	.0092	11.3
12.25	49.0	.0153	13.35		
12.50	48.5	.0142	14.35	.0080	12.8
12.75	48.5	.0115	15.20		
13.00	48.5	.0130	15.62	.0069	14.4
13.25	48.5	.0103	16.05		
13.50	49.0	.0106	16.50	.0086	15.8
13.75	49.5	.0161	17.00		
14.00	49.0	.0117	17.65	.0089	17.9
14.25	49.0	.0151	18.25		
14.50	49.0	.0119	19.10	.0096	20.2
14.75	49.0	.0161	20.70		
15.00	49.0	.0122	22.25	.0085	23.1
15.25	49.0	.0133	23.85		
15.50	49.0	.0035	25.40	.0016	26.0
15.75	49.0	.0099	27.05		
16.00	49.5	.0123	28.50	.0074	26.7
16.25	49.5	.0109	29.60		
16.50	49.5	.0115	30.70	.0033	29.6
16.75	50.0	.0046	31.80		
17.00			32.40		31.0

TABLE 7. The GROWTH input data and the corresponding simulated growth of coho salmon from the 1968 brood graded into four size groups and reared at WDF Klickitat hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Very small grade, FHMCT = .72					
7.00	50.5	.0288	1.58	.0187	1.58
7.25	51.0	.0285	1.80		
7.50	51.0	.0339	2.02	.0232	2.05
7.75	51.0	.0348	2.30		
8.00	51.0	.0326	2.63	.0233	2.84
8.25	51.0	.0369	3.15		
8.50	50.0	.0246	3.68	.0149	3.93
8.75	50.5	.0212	4.27		
9.00	51.0	.0247	4.83	.0144	4.85
9.25	50.5	.0196	5.10		
9.50	50.5	.0177	5.40	.0100	5.9[illegible]
9.75	50.5	.0159	6.00		
10.00	51.0	.0167	6.58	.0093	6.82
10.25	50.5	.0152	7.25		
10.50	50.0	.0198	7.88	.0126	7.77
10.75	49.0	.0191	8.18		
11.00	49.5	.0223	8.50	.0144*	9.28
11.25	49.0	.0217	8.80		
11.50	49.0	.0215	9.25	.0088	10.4 *
11.75	50.0	.0077	10.35		
12.00	49.0	.0124	11.45	.0076	11.8
12.25	49.0	.0136	12.10		
12.50			12.80		13.1

* predicted values for the simulation restart at 11.00.

TABLE 7. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Small grade					
7.00	50.5	.0199	2.66	.0131	2.66
7.25	51.0	.0185	3.00		
7.50	51.0	.0245	3.33	.0172	3.20
7.75	51.0	.0219	3.73		
8.00	51.0	.0198	4.12	.0134	4.06
8.25	51.0	.0182	4.50		
8.50	50.0	.0149	4.86	.0092	4.91
8.75	50.5	.0139	5.20		
9.00	51.0	.0148	5.52	.0090	5.58
9.25	50.5	.0137	6.00		
9.50	50.5	.0148	6.48	.0092	6.33
9.75	50.5	.0136	7.05		
10.00	51.0	.0152	7.42	.0094	7.20
10.25	50.5	.0132	8.55		
10.50	50.0	.0149	9.27	.0103	8.21
10.75	49.0	.0146	9.48		
11.00	49.5	.0180	9.70	.0130	9.48
11.25	49.0	.0175	10.02		
11.50	49.0	.0181	10.40	.0128	11.4
11.75	50.0	.0168	11.20		
12.00	49.0	.0122	12.00	.0092	13.6
12.25	49.0	.0141	12.65		
12.50			12.95		15.5

TABLE 7. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Large grade					
7.00	50.5	.0104	3.70	.0037	3.70
7.25	51.0	.0099	3.88		
7.50	51.0	.0118	4.10	.0053*	3.90
7.75	51.0	.0111	4.38		
8.00	51.0	.0117	4.66	.0055	4.42*
8.25	51.0	.0113	4.83		
8.50	50.0	.0148	5.02	.0092	4.77
8.75	50.5	.0141	5.30		
9.00	51.0	.0149	5.60	.0089	5.43
9.25	50.5	.0135	6.20		
9.50	50.5	.0147	6.72	.0094	6.14
9.75	50.5	.0141	7.05		
10.00	51.0	.0147	7.40	.0093	7.01
10.25	50.5	.0136	8.04		
10.50	50.0	.0148	8.63	.0099	7.98
10.75	49.0	.0139	9.18		
11.00	49.5	.0180	9.70	.0122	9.16
11.25	49.0	.0156	11.15		
11.50	49.0	.0179	12.35	.0128	10.9
11.75	50.0	.0171	12.92		
12.00	49.0	.0120	13.50	.0086	13.0
12.25	49.0	.0131	14.05		
12.50			14.63		14.7

* predicted values for the simulation restart at 7.50.

TABLE 7. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Extra large grade					
7.00	50.5	.0079	5.68	.0015	5.68
7.25	51.0	.0074	6.02		
7.50	51.0	.0089	6.32	.0029	5.80
7.75	51.0	.0088	6.35		
8.00	51.0	.0092	6.40	.0032*	6.04
8.25	51.0	.0088	6.66		
8.50	50.0	.0089	6.88	.0035	6.69*
8.75	50.5	.0089	6.88		
9.00	51.0	.0089	6.95	.0030	7.03
9.25	50.5	.0082	7.50		
9.50	50.5	.0077	8.05	.0019	7.33
9.75	50.5	.0073	8.40		
10.00	51.0	.0077	8.77	.0019	7.52
10.25	50.5	.0074	9.15		
10.50	50.0	.0148	9.48	.0102	7.72
10.75	49.0	.0147	9.57		
11.00	49.5	.0179	9.75	.0126	8.91
11.25	49.0	.0167	10.45		
11.50	49.0	.0177	11.15	.0124	10.6
11.75	50.0	.0162	12.15		
12.00	49.0	.0120	13.10	.0093	12.6
12.25	49.0	.0145	14.00		
12.50			14.90		14.4

* predicted values for the simulation restart at 8.00.

TABLE 8. The GROWTH input data and the corresponding simulated growth for the lot of coho salmon from the 1968 White River brood reared at the WDF Minter Creek hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
5.00	49.5	.0274	.46	.0145	.460
5.25	49.5	.0248	.51		
5.50	52.0	.0219	.58	.0116	.563
5.75	51.0	.0269	.66		
6.00	53.5	.0290	.74	.0237	.663
6.25	51.5	.0415	.86		
6.50	55.5	.0310	1.06	.0213	.925
6.75	56.0	.0376	1.30		
7.00	57.0	.0202	1.45	.0121	1.25
7.25	53.5	.0302	1.51		
7.50	53.0	.0426	1.65	.0282	1.48
7.75	53.0	.0336	2.10		
8.00	53.5	.0360	2.45	.0246	2.19
8.25	53.5	.0312	2.75		
8.50	53.0	.0322	3.10	.0206	3.09
8.75	52.5	.0250	3.55		
9.00	52.5	.0236	4.00	.0158	4.13
9.25	52.5	.0228	4.45		
9.50			4.60		5.15
10.50	51.5	.0145	7.10	.0210	7.10
10.75	50.5	.0166	7.80		
11.00	47.5	.0105	8.55	.0148	8.07
11.25	45.0	.0082	9.00		
11.50	46.0	.0069	9.50	.0145	8.55
11.75	46.5	.0119	9.85		
12.00	47.5	.0082	9.90	.0148	9.09
12.25	46.0	.0096	9.95		
12.50	44.5	.0074	9.99	.0117	9.56
12.75	43.5	.0072	10.00		
13.00	41.5	.0062	10.10	.0099	9.96
13.25	43.0	.0069	10.50		
13.50	43.0	.0090	10.90	.0105	10.3
13.75	43.0	.0079	11.25		
14.00	42.5	.0067	11.65	.0080	11.1
14.25	38.5	.0060	11.95		
14.50	40.0	.0078	12.05	.0088	11.6
14.75	43.0	.0067	12.15		
15.00			12.50		12.3

TABLE 9. The GROWTH input data and the corresponding simulated growth for a pond of coho salmon in the production lot of the 1969 brood reared at the WDF Minter Creek hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
7.00	52.0	.0261	2.52	.0182	2.52
7.25	53.5	.0271	3.10		
7.50	52.5	.0195	3.55	.0088	3.25
7.75	54.5	.0170	4.20		
8.00	55.0	.0187	4.72	.0113	3.68
8.25	54.5	.0227	5.00		
8.50	52.0	.0240	5.28	.0137	4.31
8.75	54.0	.0187	5.63		
9.00	54.5	.0170	6.22	.0073	5.22
9.25	53.0	.0155	6.82		
9.50	53.5	.0168	7.43	.0060	5.80
9.75	53.5	.0145	8.17		
10.00	50.5	.0133	8.90	.0020	6.43
10.25	50.0	.0122	9.68		
10.50	49.5	.0113	10.45	-.0016	6.93
10.75	51.0	.0076	11.10		
11.00	48.5	.0056	11.17	-.0008*	7.19
11.25	48.0	.0056	11.25		
11.50	47.0	.0037	11.32	.0005	11.1 *
11.75	43.5	.0074	11.40		
12.00	45.0	.0092	11.48	.0027	11.2
12.25	45.5	.0055	11.57		
12.50	45.5	.0048	11.64	.0004	11.6
12.75	41.5	.0049	11.64		
13.00	41.5	.0047	11.64	.0002	11.6
13.25	42.5	.0039	11.64		
13.50	40.5	.0032	11.64	.0001	11.7
13.75	38.5	.0040	11.67		
14.00	39.5	.0050	11.83	.0047	11.7
14.25	38.5	.0089	12.00		
14.50	39.0	.0068	12.15	.0047	12.5
14.75	40.0	.0073	12.32		
15.00	42.0	.0134	12.48	.0083	13.3
15.25	42.5	.0115	12.70		
15.50	40.5	.0070	13.28	.0082	15.0
15.75	43.5	.0183	14.00		
16.00	42.0	.0141	15.45	.0067	16.8
16.25	38.5	.0073	17.00		
16.50	40.5	.0073	18.70	.0060	18.5

* predicted values for the simulation restart at 11.00.

TABLE 9. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
16.75	42.0	.0103	19.85		
17.00	43.0	.0114	20.50	.0082	20.1
17.25	44.0	.0136	21.15		
17.50			22.00		22.5

TABLE 10. The GROWTH input data and the corresponding simulated growth for two lots of coho salmon from the 1968 brood reared at the WDF Minter Creek hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
OPR diet trial					
7.50	53.0	.0334	2.10	.0221	2.10
7.75	53.0	.0284	2.45		
8.00	53.5	.0333	2.80	.0202	2.86
8.25	53.5	.0238	3.25		
8.50	53.0	.0293	3.70	.0178	3.80
8.75	52.5	.0215	4.20		
9.00	52.5	.0222	4.75	.0172	4.87
9.25	52.5	.0263	5.40		
9.50	51.0	.0278	6.05	.0179	6.20
9.75	51.0	.0220	6.85		
10.00	51.0	.0204	7.60	.0144	7.96
10.25	50.5	.0205	7.95		
10.50	51.5	.0153	8.45	.0088	9.75
10.75	50.5	.0141	9.80		
11.00	47.5	.0101	10.82	.0045	11.0
11.25	45.0	.0083	10.88		
11.50	46.0	.0072	10.95	.0051	11.7
11.75	46.5	.0122	11.02		
12.00	47.5	.0065	11.08	.0040	12.6
12.25	46.0	.0111	11.15		
12.50	44.5	.0092	11.22	.0042*	13.4
12.75	43.5	.0073	11.30		
13.00	41.5	.0072	11.42	.0036	11.9 *
13.25	43.0	.0070	12.10		
13.50	43.0	.0084	12.78	.0042	12.5
13.75	43.0	.0072	13.45		
14.00	42.5	.0061	14.13	.0032	13.3
14.25	38.5	.0061	14.67		
14.50	40.0	.0080	14.83	.0043	13.9
14.75	43.0	.0066	15.00		
15.00			15.25		14.7

* predicted values for the simulation restart at 12.50.

TABLE 10. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
ADP diet trial					
7.50	53.0	.0245	2.10	.0187	2.10
7.75	53.0	.0206	2.50		
8.00	53.5	.0295	2.90	.0219	2.73
8.25	53.5	.0210	3.35		
8.50	53.0	.0242	3.85	.0174	3.70
8.75	52.5	.0170	4.55		
9.00	52.5	.0176	5.15	.0176	4.72
9.25	52.5	.0235	5.50		
9.50	51.0	.0263	5.90	.0183	6.04
9.75	51.0	.0182	6.80		
10.00	51.0	.0158	7.65	.0128	7.80
10.25	50.5	.0151	8.40		
10.50	51.5	.0113	9.15	.0075	9.33
10.75	50.5	.0106	9.80		
11.00	47.5	.0083	10.35	.0041	10.4
11.25	45.0	.0059	10.55		
11.50	46.0	.0058	10.70	.0051	11.0
11.75	46.5	.0098	10.90		
12.00	47.5	.0051	11.25	.0036*	11.8
12.25	46.0	.0085	11.60		
12.50	44.5	.0069	11.95	.0036	11.8 *
12.75	43.5	.0053	12.30		
13.00	41.5	.0052	12.65	.0044	12.5
13.25	43.0	.0073	12.95		
13.50	43.0	.0098	13.30	.0073	13.2
13.75	43.0	.0086	13.65		
14.00	42.5	.0074	13.95	.0046	14.7
14.25	38.5	.0044	14.25		
14.50	40.0	.0057	14.55	.0035	15.6
14.75	43.0	.0048	14.85		
15.00			15.30		16.4

* predicted values for the simulation restart at 12.00.

TABLE 11. The GROWTH input data and the corresponding simulated growth of the coho salmon from the 1970 brood reared at the FCO Sandy River hatchery and fed the OPR diet and then the ADP diet.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
OPR diet					
9.00	65.5	.0241	7.60	.0072	7.60
9.25	61.2	.0220	8.75		
9.50	59.9	.0201	9.65	.0081*	8.41
9.75	57.2	.0162	10.55		
10.00	55.4	.0172	11.25	.0107	10.8 *
10.25	53.9	.0179	12.05		
10.50	52.6	.0170	12.85	.0109	12.6
10.75	50.8	.0158	13.65		
11.00	51.0	.0131	14.50	.0056	14.6
11.25	51.9	.0100	15.65		
11.50	45.7	.0111	16.75	.0074	15.8
11.75	44.6	.0115	17.85		
12.00			19.00		17.6
ADP diet					
12.50	44.9	.0078	19.50	.0054	19.5
12.75	44.3	.0057	19.65		
13.00	51.0	.0071	19.85	.0036	21.0
13.25	51.9	.0036	20.30		
13.50	45.7	.0042	21.00	.0011	22.1
13.75	44.6	.0026	21.75		
14.00	43.2	.0026	22.45	.0016	22.5
14.25	43.7	.0034	23.03		
14.50	44.9	.0046	22.95	.0026	23.0
14.75	44.3	.0035	22.85		
15.00	45.2	.0050	22.80	.0039	23.8
15.25	42.7	.0035	22.73		
15.50	42.4	.0031	23.05	.0022*	25.2
15.75	42.2	.0046	23.55		
16.00	38.9	.0036	24.05	.0030	23.8 *
16.25	38.9	.0054	24.55		
16.50	40.1	.0066	25.15	.0042	24.8
16.75	42.0	.0051	25.80		
17.00	38.6	.0066	26.45	.0044	26.3
17.25	35.6	.0048	27.10		
17.50			27.80		28.0

* predicted values for the simulation restart at 9.50 and 15.50.

TABLE 12. The GROWTH input data and the corresponding simulated growth of the coho salmon in lot 2 of the 1969 brood and lot 1 of the 1970 brood reared at the FCO Cascade hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
1969 brood lot 2					
5.00	41.9	.0329	.805	.0169	.805
5.25	41.1	.0222	.920		
5.50	43.9	.0275	1.05	.0180	1.02
5.75	43.2	.0317	1.25		
6.00	47.2	.0309	1.40	.0188	1.31
6.25	47.8	.0311	1.60		
6.50	51.0	.0283	1.80	.0194	1.71
6.75	51.7	.0364	2.10		
7.00	51.1	.0404	2.40	.0254	2.24
7.25	59.9	.0404	2.70		
7.50	55.9	.0494	3.00	.0295	3.20
7.75	60.9	.0444	3.55		
8.00	57.8	.0380	4.20	.0222*	4.83
8.25	58.4	.0356	4.85		
8.50	55.0	.0311	5.55	.0191	5.73*
8.75	57.0	.0311	6.35		
9.00	57.4	.0282	7.50	.0163	7.49
9.25	56.9	.0279	8.70		
9.50	57.4	.0249	9.90	.0152	9.41
9.75	55.9	.0271	11.05		
10.00	51.5	.0265	12.10	.0156	11.6
10.25	49.4	.0247	13.00		
10.50	48.5	.0230	13.95	.0126	14.5
10.75	51.0	.0185	14.90		
11.00	50.1	.0185	16.00	.0107	17.3
11.25	48.4	.0171	17.30		
11.50	47.4	.0113	18.65	.0058	20.1
11.75	43.9	.0106	19.95		
12.00	44.2	.0079	21.30	.0031	21.8
12.25	45.9	.0079	21.70		
12.50	45.0	.0067	22.15	.0013	22.7
12.75	40.0	.0040	22.55		
13.00	39.7	.0040	23.00	.0005	23.2
13.25	41.4	.0042	23.16		
13.50	39.8	.0048	23.16	.0015	23.4
13.75	37.8	.0039	23.16		
14.00	38.5	.0039	23.16	-.0009	23.8
14.25	35.5	.0009	23.20		

* predicted values for the simulation restart at 8.00.

TABLE 12. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
1969 brood lot 2 - continued					
14.50	38.1	.0036	23.45	.0007	23.6
14.75	40.9	.0043	23.70		
15.00	40.9	.0051	23.95	.0017	23.8
15.25	41.1	.0053	24.20		
15.50	39.1	.0052	24.60	.0023	24.4
15.75	42.4	.0061	25.05		
16.00			25.45		25.2
1970 brood lot 1					
5.50	44.6	.0307	.85	.0181	.85
5.75	45.0	.0294	1.10		
6.00	44.2	.0276	1.30	.0170	1.09
6.25	46.9	.0295	1.50		
6.50	44.9	.0249	1.80	.0180	1.39
6.75	47.6	.0345	2.00		
7.00	47.9	.0413	2.30	.0259	1.79
7.25	50.8	.0426	2.60		
7.50	49.0	.0425	2.95	.0249	2.57
7.75	51.4	.0386	3.30		
8.00	53.7	.0417	3.80	.0262	3.64
8.25	60.0	.0407	4.30		
8.50	61.6	.0285	4.75	.0151	5.26
8.75	61.8	.0367	5.28		
9.00	63.3	.0409	6.55	.0200	6.49
9.25	61.1	.0337	7.95		
9.50	58.8	.0316	9.30	.0180*	8.59
9.75	56.0	.0276	10.65		
10.00	53.9	.0246	11.95	.0130	12.0 *
10.25	53.6	.0192	13.15		
10.50	51.3	.0169	14.30	.0087	14.4
10.75	51.9	.0155	15.45		
11.00	50.3	.0152	16.50	.0079	16.2
11.25	51.1	.0145	17.25		
11.50	45.4	.0139	18.00	.0049	18.1
11.75	43.6	.0055	18.75		
12.00	41.9	.0115	19.50	.0065	19.4
12.25	42.4	.0109	20.25		
12.50	43.1	.0086	20.95	.0038	21.2
12.75	42.1	.0071	21.70		

* predicted values for the simulation restart at 9.50.

TABLE 12. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
1970 brood lot 1 - continued					
13.00	42.1	.0067	22.45	.0036	22.4
13.25	39.6	.0074	23.00		
13.50	39.5	.0052	23.35	.0016	23.6
13.75	41.0	.0046	23.70		
14.00	36.4	.0018	24.05	.0005	24.1
14.25	37.6	.0045	24.40		
14.50	39.4	.0046	24.44	.0006	24.3
14.75	40.6	.0033	24.46		
15.00	36.7	.0026	24.50	.0005	24.5
15.25	33.0	.0000	24.53		
15.50	36.7	.0036	24.90	.0020	24.7
15.75	40.9	.0059	25.45		
16.00	40.2	.0071	25.95	.0040	25.4
16.25	39.9	.0071	26.45		
16.50	41.1	.0069	27.15	.0011	26.9
16.75	43.1	.0028	27.95		
17.00			28.75		27.3

TABLE 13. The GROWTH input data and the corresponding simulated growth of the coho salmon in lot 2 of the 1969 brood and in lot 1 of the 1970 brood reared at FCO Bonneville hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
1969 brood lot 2					
5.50	45.2	.0484	.835	.0256	.835
5.75	44.1	.0404	1.11		
6.00	47.9	.0362	1.40	.0206	1.19
6.25	48.2	.0330	1.67		
6.50	51.3	.0250	1.97	.0195	1.59
6.75	49.5	.0419	2.30		
7.00	49.9	.0389	2.70	.0224	2.09
7.25	53.6	.0346	3.05		
7.50	50.5	.0336	3.40	.0194	2.87
7.75	53.9	.0314	4.05		
8.00	52.9	.0298	4.85	.0171	3.76
8.25	52.6	.0293	5.55		
8.50	51.7	.0275	6.50	.0155	4.78
8.75	51.9	.0260	7.30		
9.00	52.1	.0240	8.10	.0133*	5.94
9.25	51.4	.0223	8.85		
9.50	52.1	.0214	9.60	.0123	9.76 *
9.75	50.9	.0218	10.40		
10.00	49.4	.0210	11.45	.0122	11.6
10.25	47.3	.0203	12.70		
10.50	47.9	.0193	13.95	.0108	13.8
10.75	48.2	.0178	15.20		
11.00	47.2	.0156	16.30	.0083	16.0
11.25	45.9	.0142	17.15		
11.50	45.9	.0132	18.00	.0071	18.0
11.75	42.7	.0122	18.90		
12.00	43.9	.0098	19.75	.0041	19.9
12.25	45.1	.0089	20.85		
12.50	44.5	.0081	21.55	.0028	21.0
12.75	39.7	.0062	22.95		
13.00	39.7	.0063	23.35	.0027	21.9
13.25	41.4	.0066	23.55		
13.50	39.8	.0058	23.45	.0026	22.7
13.75	38.7	.0058	23.35		
14.00	38.5	.0038	23.25	.0008	23.5
14.25	37.3	.0042	23.25		
14.50	38.0	.0052	23.60	.0022	23.8

* predicted values for the simulation restart at 9.00.

TABLE 13. continued.

time computer months	temperature °F	daily ration g/g/day	observed wieght g	predicted specific growth rate g/g/day	predicted weight g
1969 brood lot 2 - continued					
14.75	40.8	.0059	24.00		
15.00	41.2	.0065	24.35	.0019	24.5
15.25	40.5	.0051	24.70		
15.50	39.8	.0050	25.60	.0008	25.2
15.75	41.2	.0045	26.55		
16.00			27.50		25.5
1970 brood lot 1					
7.00	47.0	.0319	2.35	.0214	2.35
7.25	48.7	.0393	2.65		
7.50	47.9	.0408	2.95	.0225	3.17
7.75	48.6	.0401	3.40		
8.00	50.6	.0389	3.90	.0227	4.34
8.25	54.4	.0344	4.45		
8.50	54.6	.0326	5.00	.0192*	5.97
8.75	54.1	.0311	5.60		
9.00	54.9	.0291	6.45	.0160	6.54*
9.25	52.6	.0257	7.30		
9.50	52.0	.0237	8.20	.0140	8.19
9.75	51.4	.0241	9.05		
10.00	50.0	.0250	10.00	.0143	9.96
10.25	48.6	.0226	11.10		
10.50	48.0	.0207	12.15	.0117	12.2
10.75	47.0	.0192	13.20		
11.00	48.8	.0166	14.30	.0088	14.3
11.25	47.4	.0154	15.45		
11.50	44.9	.0143	16.60	.0079	16.2
11.75	42.9	.0134	17.75		
12.00	42.2	.0114	18.90	.0060	18.1
12.25	42.9	.0104	19.50		
12.50	43.3	.0097	20.00	.0047	19.7
12.75	42.6	.0092	20.45		
13.00	42.1	.0083	20.95	.0041	21.1
13.25	39.6	.0076	21.45		
13.50	40.3	.0068	21.90	.0026	22.3
13.75	41.1	.0061	22.15		
14.00	37.6	.0047	22.85	.0023	23.1
14.25	38.9	.0056	23.30		
14.50	39.6	.0054	23.75	.0017	23.9

* predicted values for the simulation restart at 8.50.

TABLE 13. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
1970 brood lot 1 - continued					
14.75	40.6	.0053	24.20		
15.00	36.6	.0034	24.60	.0020	24.5
15.25	34.4	.0031	25.05		
15.50	38.1	.0062	25.70	.0035	25.1
15.75	40.4	.0069	26.35		
16.00	40.4	.0053	27.05	.0020	26.4
16.25	40.2	.0054	27.70		
16.50			28.35		27.1

TABLE 14. The GROWTH input data and the corresponding simulated growth for the experimental lots of coho salmon from the 1964 brood reared at FCO Big Creek hatchery.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Low ration					
5.00	50.6	.0137	2.20	.0109	2.20
5.25	44.9	.0198	2.30		
5.50	49.4	.0170	2.50	.0110	2.56
5.75	48.6	.0171	2.70		
6.00	49.6	.0168	2.93	.0116	2.99
6.25	50.6	.0185	3.12		
6.50	52.1	.0170	3.43	.0113	3.52
6.75	51.4	.0182	3.80		
7.00	52.7	.0125	4.43	.0066	4.12
7.25	54.1	.0150	4.55		
7.50	55.9	.0187	4.87	.0093	4.52
7.75	55.3	.0151	5.12		
8.00	55.1	.0205	5.35	.0106	5.14
8.25	57.1	.0156	5.58		
8.50	57.1	.0201	5.83	.0112	5.97
8.75	56.9	.0172	6.55		
9.00	56.9	.0161	7.30	.0069	6.98
9.25	55.5	.0126	8.00		
9.50	53.2	.0173	8.70	.0087*	7.70
9.75	52.9	.0110	9.20		
10.00	52.1	.0148	9.55	.0075	9.82*
10.25	50.6	.0100	9.85		
10.50	50.9	.0127	10.15	.0062	10.9
10.75	51.8	.0095	10.65		
11.00	50.6	.0130	11.55	.0062	11.9
11.25	48.4	.0081	12.45		
11.50	50.2	.0097	13.30	.0037	13.0
11.75	50.5	.0071	14.25		
12.00	48.6	.0049	14.45	.0017	13.7
12.25	48.1	.0072	14.65		
12.50	45.8	.0058	14.85	.0020	14.0
12.75	44.7	.0052	15.00		
13.00	45.9	.0046	15.08	.0016	14.4
13.25	40.4	.0046	15.10		
13.50	38.3	.0028	15.12	.0002	14.7
13.75	38.6	.0022	15.13		
14.00	39.9	.0028	15.15	.0000	14.7

*predicted values for the simulation restart at 9.50.

TABLE 14. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
Low ration - continued					
14.25	42.9	.0029	15.15		
14.50	41.0	.0041	15.16	.0012	14.[illegible]
14.75	41.1	.0035	15.17		
15.00	41.4	.0018	15.18	-.0004	15.[illegible]
15.25	41.4	.0032	15.23		
15.50	40.9	.0032	15.28	.0004	14.[illegible]
15.75	42.6	.0033	15.33		
16.00	40.1	.0039	15.38	.0014	15.0
16.25	40.9	.0038	15.80		
16.50			16.20		15.[illegible]
High ration lot					
5.00	50.6	.0270	2.20	.0170	2.20
5.25	44.9	.0295	2.45		
5.50	49.4	.0272	2.86	.0161	2.79
5.75	48.6	.0264	3.30		
6.00	49.6	.0239	3.70	.0170	3.50
6.25	50.6	.0318	4.15		
6.50	52.1	.0277	4.85	.0170	4.43
6.75	51.4	.0277	5.65		
7.00	52.7	.0200	6.45	.0118	5.62
7.25	54.1	.0228	7.20		
7.50	55.9	.0252	8.00	.0162	6.63
7.75	55.3	.0287	8.85		
8.00	55.1	.0276	9.75	.0159	8.32
8.25	57.1	.0254	10.6		
8.50	57.1	.0287	11.5	.0164	10.4
8.75	56.9	.0256	12.9		
9.00	56.9	.0253	14.5	.0156	13.1
9.25	55.5	.0258	16.0		
9.50	53.2	.0250	17.7	.0138	16.3
9.75	52.9	.0200	19.5		
10.00	52.1	.0199	21.1	.0114	19.8
10.25	50.6	.0178	22.8		
10.50	50.9	.0160	24.4	.0094	23.2
10.75	51.8	.0159	26.0		
11.00	50.6	.0176	27.8	.0095	26.4
11.25	48.4	.0146	29.4		
11.50	50.2	.0129	30.9	.0076	30.2

TABLE 14. continued.

time computer months	temperature °F	daily ration g/g/day	observed weight g	predicted specific growth rate g/g/day	predicted weight g
High ration lot - continued					
11.75	50.5	.0139	32.4		
12.00	48.6	.0085	33.2	.0035	33.6
12.25	48.1	.0078	33.9		
12.50	45.8	.0092	34.5	.0041	35.3
12.75	44.7	.0069	35.2		
13.00	45.9	.0088	35.5	.0032	37.3
13.25	40.4	.0044	35.6		
13.50	38.3	.0025	35.8	.0001	39.1
13.75	38.6	.0023	36.0		
14.00	39.9	.0014	36.3	-.0002	39.1
14.25	42.9	.0038	37.5		
14.50	41.0	.0073	38.7	.0038	39.0
14.75	41.1	.0064	39.9		
15.00	41.4	.0031	41.2	.0016	41.2
15.25	41.4	.0056	41.8		
15.50	40.9	.0055	41.9	.0027	42.1
15.75	42.6	.0057	42.0		
16.00	40.1	.0067	42.1	.0038	43.7
16.25	40.9	.0067	42.2		
16.50			42.3		46.1